THE QUARTERLY REVIEW OF BIOLOGY

SEPTEMBER
1952

Vol. 27 No. 3

Published by
THE WILLIAMS & WILKINS COMPANY
BALTIMORE, U. S. A.

Copyright 1952
THE WILLIAMS & WILKINS COMPANY

THE QUARTERLY REVIEW OF BIOLOGY

FOUNDED BY RAYMOND PEARL

B. H. WILLIER, *Editor*
The Johns Hopkins University

H. BENTLEY GLASS
Associate Editor

CARL P. SWANSON
Assistant Editor

Advisory Board

IRVING W. BAILEY ..... *Harvard University*
G. W. BEADLE ..... *California Institute of Technology*
E. G. CONKLIN ..... *Princeton University*
ROSS G. HARRISON ..... *Yale University*
LIBBIE H. HYMAN ..... *American Museum of Natural History*
A. L. KROEBER ..... *University of California*
K. S. LASHLEY ..... *Harvard University*
CHARLES W. METZ ..... *University of Pennsylvania*
THOMAS PARK ..... *University of Chicago*
G. H. PARKER ..... *Harvard University*
ALFRED S. ROMER ..... *Harvard University*
ALEX. G. RUTHVEN ..... *University of Michigan*
F. O. SCHMITT ..... *Massachusetts Institute of Technology*
PAUL WEISS ..... *University of Chicago*

Papers to Appear in an Early Number

RECENT ADVANCES IN OYSTER BIOLOGY (Concluded)
D. P. Korringa, *Government Institute for Fishery Investigations, Bergen-op-Zoom, Netherlands*

NARIAL BREATHING IN FISHES AND THE EVOLUTION OF INTERNAL NARES
James W. Atz, *New York Zoological Society*

Entered as second-class matter January 27, 1926, at the post office at Baltimore, Maryland, under the act of March 3, 1879
Subscription price $6.00 a year ($6.30 outside Postal Union) $1.75 a copy.
Made in United States of America

Annals of Eugenics

A JOURNAL OF HUMAN GENETICS

Edited by L. S. PENROSE *with the assistance of*
JULIA BELL, R. A. FISHER, J. B. S. HALDANE, MARY N. KARN, R. R. RACE, J. A. F. ROBERTS

Vol. XVII. Part 1. September 1952.

Familial intestinal polyposis. C. E. DUKES.

An A_1 *cD*^{u}*e/cde* blood in an English family. P. ASPINALL AND I. DUNSFORD.

A simplified heterogeneity test. C. A. B. SMITH.

The chromosome complement in a mongolian imbecile. M. MITTWOCH.

Albinism in South-Western Nigeria. N. A. BARNICOT.

SUBSCRIPTION (payable in advance) *$9.50 per volume of 4 parts.*

***Issued by the* CAMBRIDGE UNIVERSITY PRESS**

32 East 57th Street, New York 22, N. Y.

JOURNALS ON MICROFILM

THE WILLIAMS & WILKINS COMPANY has arranged to make available to libraries issues of certain of its periodical publications in microfilm form.

Microfilm makes it possible to produce and distribute copies of periodical literature on the basis of the entire volume in a single roll in editions of 30 or more, at a cost approximately equal to the cost of binding the same material in a conventional library binding.

Under the plan, the library keeps the printed issues unbound and circulates them in that form for from two to three years—which corresponds to the period of greatest use. When the paper copies begin to wear out, or are not called for frequently, they are disposed of and the microfilm is substituted.

Sales are restricted to those subscribing to the paper edition and the film copy is distributed only at the end of the volume year.

The microfilm is in the form of positive microfilm and is furnished on metal reels suitably labeled.

Inquiries concerning purchase should be directed to

UNIVERSITY MICROFILMS

313 N. First St. **Ann Arbor, Mich.**

(In writing to advertisers, please mention the journal—it helps.)

THE SERVALL ANGLE CENTRIFUGE
(SUPERSPEED)

Accepted and acclaimed by scientists throughout the world for its durability, safety features, smooth performance and efficiency. Our years of experience, and our pioneering of the high speed angle centrifuges guarantee their continued superiority.

Write for Bulletin R-91

Max. speed 13,500 r.p.m.
or R.C.F. 23,000 x G
Max. capacity 8 x 50cc

Ivan Sorvall, inc.

210 Fifth Avenue, New York 10, N.Y.

GENES AND MUTATIONS
Cold Spring Harbor Symposia on
Quantitative Biology

Volume XVI (1951)

540 quarto pages, with numerous figures

Authoritative reviews of the gene problem, presented in 35 papers and edited discussions. Subjects considered are: theory of the gene, cytoplasmic constituents of heredity, evolution of the gene, induction of changes in genes and chromosomes, genetic mechanisms in bacteria and bacterial viruses. Table of contents sent on request.

Previous volumes still available: IX (1941) Genes and Chromosomes; XI (1946) Heredity and Variation in Microorganisms; XII (1947) Nucleic Acids and Nucleoproteins; XIII (1948) Biological Applications of Tracer Elements; XIV (1949) Amino Acids and Proteins; XV (1950) Origin and Evolution of Man.

Prices: Volume XVI, $9.00; other volumes, $7.00. Volumes IX and XVI, or XV and XVI, $14.00; volumes IX, XV, and XVI, $20. Postage extra; domestic, 25 cents, foreign 50 cents per volume.

Address: Biological Laboratory
Cold Spring Harbor, New York

Practical... Efficient

THE SCIENTIFIC PAPER
HOW TO PREPARE IT
HOW TO WRITE IT
Second Edition

By **Sam F. Trelease,** *Columbia University*

Lightens your work, saves your money, helps you present your material in the most effective way. Gives rules based on recognized authorities.

173 pp. ***9 figs.*** ***$2.50***

The Williams & Wilkins Co.
Mt. Royal and Guilford Aves. Baltimore 2, Md.

(In writing to advertisers, please mention the journal—it helps.)

VOL. 27, NO. 3 September, 1952

THE QUARTERLY REVIEW *of* BIOLOGY

THE ENVIRONMENTAL COMPLEX IN RELATION TO PLANT GROWTH AND DISTRIBUTION

By W. D. BILLINGS

Department of Botany, Duke University

THE apparently innocuous question, "Why do plants grow where they do?" involves a number of fundamental problems in plant ecology. In this relatively young and complex science, however, this question has often been neglected in the multiplicity of problems presented to an ecologist in any region. In fairly recent times many ecologists' energies have been devoted, partially of necessity, to investigating the structure and dynamics of vegetation which is rapidly being changed or eradicated by modern civilization. This work is of great importance, but the solving of the principal problems in the relations between plant growth, distribution, and physical environments is fundamental to any understanding of plant aggregations and their changes.

In recent years, increased interest in these problems of why plants grow where they do has resulted in at least two large symposia devoted to the subject (A.A.A.S., Vancouver, B. C., June, 1949; A.I.B.S., Minneapolis, Minn., September, 1951). These symposia are but surface evidence of current attempts to solve complex ecological problems by understanding the environmental relationships of the various species of importance in particular vegetations. These large problems are far from solution. However, it is the purpose of the present paper to bring together some of the recent ideas and work in the widely scattered fields of plant ecology and its underlying sciences, with the hope that such a synthesis will help to show in what directions future research in ecology is needed. It is patently impossible to cover such a large subject in small space, therefore the emphasis will be on certain ideas and concepts basic to an understanding of the complex plant-environment relations and the significance of these relations in the structure and interpretation of vegetation.

STRUCTURE OF THE ENVIRONMENT

It is not the purpose of this short review to detail thoroughly the nature of environmental responses in plants and vegetation. This has been done far more completely in recent textbooks by Cain (1944), Daubenmire (1947), Oosting (1948), and in particular detail by Lundegårdh (1949). However, it is necessary to give in a general way the structure of a plant environment so that its complexity can be better understood.

Factoring the Environment

The environment of a plant may be defined as the sum of all external forces and substances affecting the growth, structure, and reproduction of that plant. The environment provides the organism with its heat, light, water, elements, and compounds. If these are available in sufficient amounts and at the right time to satisfy the growth and reproduction requirements of any of the ecotypes or biotypes of a species, that species can grow

there provided its seeds and propagules can get there.

Since the environment is a complex, it has been customary for ecologists and plant physiologists to break it up arbitrarily into factors and to study the effect of such single factors on the plant. This is a somewhat artificial, but probably necessary, method of attack, since in nature it is almost impossible for one factor to change without affecting others. Yet if such an analytical approach is followed, each factor must be evaluated in relation to all of the other factors, and the analysis must be followed by a synthesis of the total results.

In an analytical approach, it is perhaps best to subdivide the environment first into large groups of factors and then to subdivide these to show the great ramification which a thorough investigation of the environment entails. Table 1 presents a more or less arbitrary subdivision of the environment into the principal groups of factors and shows how they may be subdivided into individual factors, factor subdivisions, and various aspects. Many things make up an environment, and an almost infinite degree of analytical breakdown is possible. However, this table can be considered as a guide to the types of growth and distribution factors which are at present being investigated by plant scientists. Unfortunately, papers dealing with the interrelations of two or more factors with the plant are few, and even fewer are the attempts to analyze and synthesize complete plant or biotic environments. Outstanding among these are the works of Lindeman (1941a, 1941b, 1942) on aquatic ecosystems using energy relationships during succession as a basis. For terrestrial communities, one of the best is the recent paper by Platt (1951) on the environmental relations of the Pennsylvania shale-barren communities.

Principle of the Holocoenotic Environment

Even though it is possible to analyze a plant environment and to study the effects of single factors on the plant, it has long been recognized by some ecologists, but not by all, that the environment-plant system is a dynamic unit in itself and reacts as a whole. Cooper (1926) viewed the vegetation of the earth as a flowing, braided stream governed and directed by all environmental factors at all times. Billings (1938) emphasized that successional changes in vegetation cannot be interpreted in terms of one factor, but only by considering the environmental complex as a whole. This principle has been termed that of the holocoenotic environment by Allee and Park (1939), and has been restated and emphasized by Cain (1944). The holocoenotic principle is fundamental to any understanding of environment-plant relationships. Complete explanations of ecological phenomena are not possible without it.

The complexity of the interrelationships between the plant and its environment and between the various factors of the environment is almost enough to discourage any attempts at complete analysis and synthesis. In fact, Cain (1944) has stated that such ecological problems not only may be difficult to solve but may really be insoluble in a mathematical sense. However, attempts by ecologists should be and are being made (Lindeman, 1942; Major, 1951).

It would be of some help in understanding the holocoenotic principle to be able to visualize the principal interactions in the environment. Fig. 1 is a diagrammatic attempt to show such an environment and the interactions between the various factors themselves and between these factors and a plant. The factors in this diagram are large units and there has been some lumping of factors in order to simplify it. Furthermore, the fifteen factors are not of equal weight. Nevertheless, the relations in a complete environment are shown in the diagram. Some biologists would consider time as an environmental factor, but time might better be considered not as a factor in itself but as a dimension by which all other factors are qualified. Therefore, time is indicated around the edge of the diagram as affecting all of the reactions within the environment.

Limiting Factors and Trigger Factors

A second principle of environment which has been far more widely used than that of the holocoenotic environment is the principle of limiting factors. This stems from the work of Liebig (1843) working with agricultural plants and soils, and has been widely adapted and adopted by ecologists during the last half-century. The thesis of this principle is that plant growth and distribution are limited when any factor in the environment falls below the minimum required by that particular species. Actually, a plant may be limited not only when a factor goes below the minimum but when it goes over the maximum tolerance by the plant for that factor. In any case, a single factor can often limit the growth, reproduction, or distribu-

TABLE 1

Factors of a Terrestrial Plant Environment

GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Climatic	Radiation	Solar radiation	Wave-lengths Intensity Photoperiod and other cycles
		Cosmic radiation	Wave-lengths Intensity Cycles
		Terrestrial radiation	Wave-lengths Intensity Cycles
	Temperature	Air temperature	Degree Cycles Lateral variation Vertical variation
		Soil temperature	Degree Cycles Freezing and thawing Lateral variation Vertical variation
		Rock and parent material temperature	Degree Cycles Freezing and thawing Lateral variation Vertical variation (geothermal gradient)
	Water	Water vapor	Amounts Vapor pressure Vapor pressure deficit Evaporation Transpiration
		Condensed water	Cloud Fog
		Precipitation	Types Amounts Frequency Snow cover
		Soil water	Soil moisture Hygroscopic water Capillary water Water table
	Atmospheric gases	Composition	CO_2 content O_2 content Other gases

TABLE 1—*Continued*

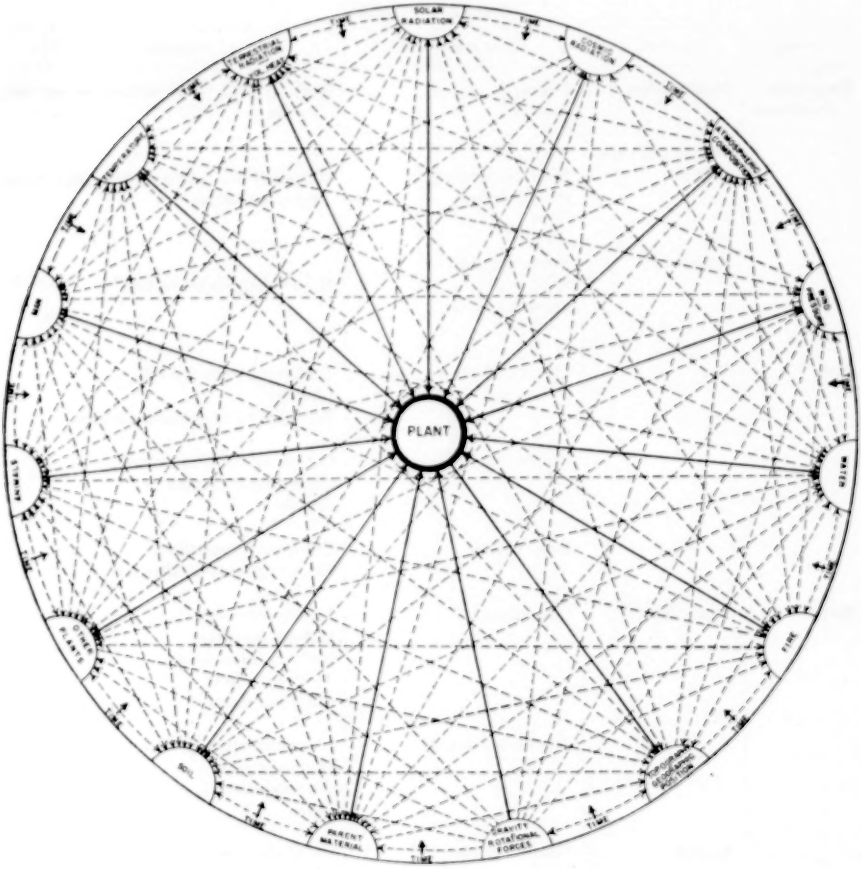
GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Climatic (*continued*)	Atmospheric gases (*continued*)	Pressure	Altitude Local pressure differences Cyclones
		Wind	Frequency Force Direction Abrasive agents
Edaphic	Parent material	Acid materials	Minerals present Structure Weathering susceptibility
		Basic materials	Minerals present Structure Weathering susceptibility
	Soil	Physical properties	Profile Structure Texture Soil moisture Soil air
		Chemical properties	Clay minerals Base exchange properties pH Anions Organic compounds
		Biotic properties	Soil flora Soil fauna Litter and humus Antibiotic effects
Geographic	Gravity	Internal effects	Hormone effects Translocation
		External effects	Isostasy Fruit and seed dispersal Runoff Landslides
	Rotational effects	Coriolis force	Works through other factors
	Geographic position	Latitude Longitude Distance and direction from coast	Work through other factors
	Vulcanism	Thermal effects	See temperature
		Mechanical effects	Ash cover Lava flows Gas explosions

TABLE 1—*Continued*

GROUPS	FACTORS	FACTOR SUBDIVISIONS	ASPECTS
Geographic (*continued*)	Diastrophism	Folding Faulting	Work through other factors except very locally
	Erosion and deposition	Water Snow (avalanches) Ice (glaciation) Wind	May affect plants directly or through changing other factors
	Topography	Slope direction Slope angle Elevation	Work through other factors
Pyric	Fire	Climatic effects	Temperature (air and soil) Intensity Post-burning microclimatic effects
		Edaphic effects	Organic matter destruction Soil structure changes Erosion
		Biotic effects	Community composition Animal populations after fire
Biotic	Other plants	Competition	Light competition Water competition Nutrient competition Antibiotic effects Autotoxic effects
		Dependence effects	Litter and humus Physical effects Chemical effects Cover
	Animals	Destructive effects	Use of plant as food, etc. Effects on soil
		Beneficial effects	Fruit and seed dispersal Nutrient effects
	Man	Can change almost any factor, at least locally	

tion of a single plant species. Cain (1944) has stated that physiological processes are multi-conditioned. He says that it is impossible to speak of a single condition of a factor as being the cause of an observed effect in an organism. In other words, since the environment is holocoenotic, Cain believes that it is erroneous to speak of a single condition of a single factor as being limiting. Major (1951) has indicated that his methods of environment-vegetation analysis on the basis of factors as independent variables may appear to contradict Cain's statements. However, since Major is using the term "independent variable" in the mathematical sense, this is only an apparent contradiction.

Actually, it seems perfectly reasonable to assume that the principle of the holocoenotic environment and the principle of limiting factors are



A HOLOCOENOTIC ENVIRONMENTAL COMPLEX

FIG. 1. DIAGRAMMATIC REPRESENTATION OF AN ENVIRONMENTAL COMPLEX

Solid lines show factor-plant relationships. Dashed lines show relations between factors. Arrows show the general direction of the effect. If the effect is reciprocal, arrows are placed at both ends of the line. Time is indicated by short inward-pointing arrows just inside the border of the diagram. The only group of factors not affecting the plant directly is that of topography and geographic position. These affect the plant only through other factors.

compatible. For example, water, or rather lack of water, is a principal limiting factor in semi-arid and arid regions. If water is added to desert adjoining cultivated land, the native desert plants are soon replaced by adventive weeds and other plants from nearby irrigated areas. These plants are kept out of the desert environments by lack of water even though their seeds arrive in the area every year. As soon as the water content of the soil is brought above the adventives' minimum requirements, however, their seedlings survive, grow, and reproduce. Certainly the addition of water has far-reaching effects in the desert environment because this environment is holocoenotic, but lack of water is the *limiting* factor and no addition of any other factor to the desert environment will

result in the same change in vegetation. Of course, the amount of water available to the adventives might be increased by eliminating the competition provided by the native plants. If the water is added permanently, the whole desert environment goes through a change—a change which results in an entirely different vegetation. When a limiting factor, then, is changed in nature and sets off a chain reaction in the ecosystem, it might well be termed a "trigger" factor. The delicate balance of an ecosystem in dynamic equilibrium and the possible far-reaching effects of even small changes have been clearly stated by Cooper (1926) and Billings (1938). Allee et al. (1949) use drought as an example of a "trigger" factor in the emigration of muskrat populations based upon the work of Errington (1939).

Numerous examples can be found to illustrate the effects of "trigger" factors in vegetation. One of the best is provided by the change from bunchgrass-sagebrush to cheatgrass (*Bromus tectorum*) over great areas in the semi-arid portions of the Great Basin of western North America. This change, which has taken place in less than 100 years, was undoubtedly triggered by the introduction of domestic grazing animals. The probable course has been an initial weakening and elimination of the more palatable bunchgrasses, followed by an increase in density of the less palatable shrubs, particularly *Artemisia tridentata*, the big sagebrush. This open community of relatively deep-rooted shrubs was invaded late in the 19th century by *Bromus tectorum*, cheatgrass, introduced accidentally from Europe. This grass spread rapidly under and between the shrubs by utilizing the soil moisture in the upper part of the soil. Through most of the region it acts as a winter annual, germinating with the first heavy fall rains and going through the winter as a seedling. In the spring it grows rapidly, flowering in May, producing ripe seed in June, and then dying and becoming dry in most places by the end of that month. From then until fall it constitutes a critical fire hazard not present in the original vegetation. Range fires have become much more frequent and cover greater areas because of the inflammable character of this dry annual. By the time of burning most of the *Bromus* seeds are on the ground and those not near to the heat of the burning shrubs survive to allow the cheatgrass to pioneer in the newly burned area. Within two or three years the burn is practically a pure stand of annual grass readily susceptible to further burning and deterioration. Recovery by shrubs is slow, the principal ones in the early stages being species of *Ephedra*, *Tetradymia*, and *Prunus* which can send up root sprouts. Sagebrush must reinvade by seed. One of the best browse shrubs, *Purshia tridentata*, is generally eradicated permanently by fire in the western Great Basin because it rarely root-sprouts in that region and its seeds are not particularly mobile. However, Blaisdell (1950) in eastern Idaho has reported that *Purshia* in that region is able to sprout and can survive unless the fire is too severe. As a result of the chain reaction started almost a century ago, the sagebrush-grass ecosystem is still out of equilibrium, and the end is not yet in sight. Perhaps man can take advantage of the situation and divert the chain back toward some sort of equilibrium by replanting perennial grasses on the burned areas, as the work of Robertson and Pearse (1945) has shown, and by proper ecological management of areas not yet in stages of extreme deterioration.

When change in a trigger factor upsets the delicate balance in an ecosystem, it is usually not possible to tell when and where the chain reaction will end. The accidental introduction of an aggressive adventive at an opportune time can greatly increase the speed and permanence of the change and thus affect the distribution of hundreds of species of native plants. This has happened in the case of the *Bromus* invasion in the intermountain region, as described above. Many of the native perennials are being killed out by the repeated fires, and some are probably doomed to extinction.

A good example of the impossibility of predicting the trend in an upset ecosystem is the present occupancy of much valuable winter range in northeastern Nevada, southern Idaho, and northern Utah by *Halogeton glomeratus*. This very poisonous plant was accidentally introduced in the middle 1930's into areas already in a disturbed state, probably due to the trigger of overgrazing. No one could have predicted the present state of these winter ranges even as late as 1935, because the biotic potential of *Halogeton* was not recognized. Now thousands of acres of valuable winter range are not only useless but a very real danger to stock because of the pure stands of *Halogeton* now occupying them. Where this destructive change will end cannot be predicted with certainty at present, but applied ecological methods can help to divert

it in the direction of proper use and some type of recovery.

Environmental Variation in Time and Space

The environment of any individual plant or local population varies not only in space but also in time. Taylor (1934) has emphasized the importance of environmental extremes in determining not only plant distributional limits but also certain geologic and edaphic features in the environment itself. He has restated Liebig's Law of the Minimum in the following terms: "The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in minimal quantity during the most critical season of the year, or during the most critical year or years of a climatic cycle." Time, like space, is then seen to be a dimension of an environment allowing or limiting the growth of individuals and local populations depending on the values of critical factors at critical times.

The environment of an individual is continually changing throughout its lifetime. Some of this change is cumulative and some is cyclic. If a factor becomes critical simultaneously with a critical stage in the life cycle of the plant, death of the individual or of many individuals in the local population may result. This may occur, of course, at any period of the life cycle, but at certain times the impact of a critical environmental extreme has greater effect. Germination, the young seedling stage, flowering, and fruiting are the stages most likely to affect plant distribution if they are disturbed or stopped by an extreme or unusual condition in the environment.

Normal growth and reproduction of a plant is genetically adapted to the changes of the environment usually encountered by the plant during its life from germination to fruiting and seed dispersal. Some degree of aberrancy in the environmental cycles and totals is to be expected. A species of wide tolerance range can survive these either in space or time. There are limits, however, beyond which even widely distributed species cannot go. These occur principally near the limits of distribution, and if they occur often enough they will keep the species from spreading farther. Endemic species have relatively narrow tolerance ranges in both space and time, and are limited to areas where the total environment and its cycles are just exactly what its gene-operated physiological processes need for successful growth and reproduction. Boyko (1949), recognizing the importance of environmental extremes in plant distribution, has introduced a useful concept which he calls the *IF* threshold of a species in which *I* indicates the intensity of a limiting factor and *F* the time-frequency of its occurrence.

Fig. 2 diagrammatically illustrates how an environment could change during the life span of a hypothetical annual plant. Starting at time zero (zygote), this plant's environment would show certain combinations and rhythms of factors *A*, *B*, *C*, *D*, *E*, *F*, and *G*. These would probably not in most cases make up the best environment for seed germination for the species but by time *X* the environment has changed enough (and perhaps affected the seed enough as, for example, in low temperature after-ripening) to allow germination with combined values and rhythms of *A′*, *B′*, *C′*, *D′*, *E′*, *F′*, and *G′*. This could be shown at any time during the life of the plant. The change in the environment and its effect on the plant could continue to successful production of seed provided no factor exceeded the tolerance limits determined by the gene structure of the plant. If this occurs, the individual might die or grow so slowly as to be out of phase with the environmental march and thus fail to reproduce.

ENVIRONMENT-PLANT COMPLEX

From the standpoint of ecology, no study of the environment alone can be very significant. The attempt must always be made to correlate or integrate the changes in the environment in time and space with the individual plants or vegetation with which it is intimately associated. The growth and distribution of plants are governed by this interaction of gene mechanism and environment.

Tolerance Range Studies

According to Good's (1931) Theory of Tolerance, a plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions, such a range representing the tolerance of the species to these external conditions. The tolerance of a species is, according to Good, subject to the laws and processes of organic evolution in the same way as its morphological characters, but the two are not necessarily linked. In other words, Good correctly views the successful functioning of a plant in a particular type of environment to be the result of genetically determined tolerance limits. Mason (1936) has amplified

Good's theory in several ways, with particular emphasis on the limiting effects of narrower tolerance ranges during critical times in the life history of a plant. Cain (1944) and Good (1947) have further extended and expanded the Theory of Tolerance until it is now one of the foundations of modern plant geography.

Since individual plants of one or more species are the building blocks of vegetation, it is a serious handicap to ecologists and to other scientists concerned with pure and applied problems in plant distribution not to have available concrete data on the tolerance ranges of the more important plants of a region. The work of agronomists and plant physiologists has provided much of this type of information for cultivated plants. To a lesser extent, foresters have information of this kind for the principal forest trees. For the great majority of wild plants, however, few or no data on tolerance ranges exist. This lack of fundamental information on the ecology of individual species has long been recognized by some ecologists, and there exist a number of papers detailing to some extent the ecology of certain species in certain regions. However, since the tolerance of a plant varies with time through its life-cycle, it was suggested as long ago as 1928 by Salisbury that the British Ecological Society should undertake to study and publish ecological life histories of the important plants of the British Isles. This suggestion led to the initiation of such a series in 1941; and within the last ten years a number of papers have been published in the *Journal of Ecology* giving the ecological fundamentals for some of the important wild plants of the British Isles.

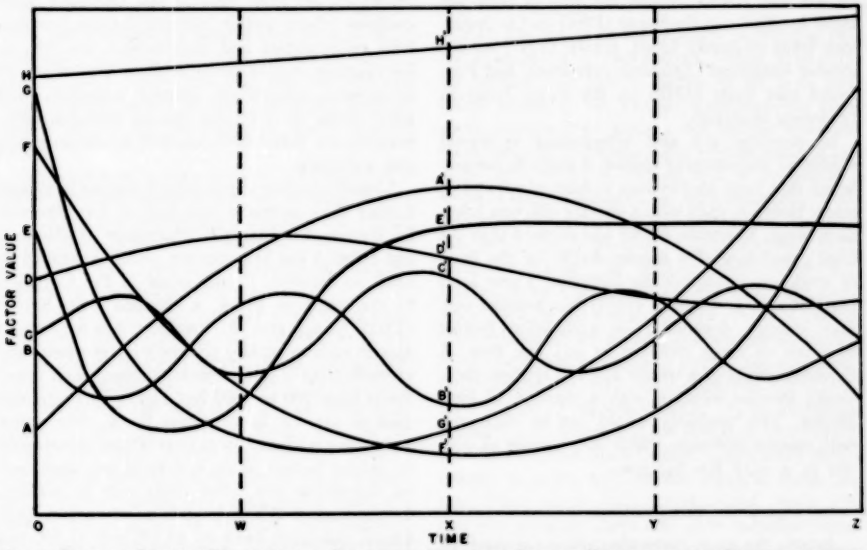


FIG. 2. DIAGRAM SHOWING HYPOTHETICAL CHANGES IN VALUES OF SEVERAL ENVIRONMENTAL FACTORS (A, B, C D, E, F, G, H) THROUGH TIME IN THE LIFE OF AN ANNUAL PLANT

Time O (zygote), time W (dormancy), time X (germination), time Y (vegetative growth), and time Z (flowering) each show different combinations of values. Factor A would become A′ at time X, factor B, B′, etc. Some factor changes are cyclic, some cumulative.

The need for this type of autecological work in North America was seen by several ecologists. Among them, D. B. Lawrence at the University of Minnesota, has used the ecological life history approach in his course in Experimental Ecology (Lawrence, 1947). In 1947, the Ecological Society of America established a committee on ecological life histories, with Lawrence as chairman. This committee has encouraged the publication of suggested outlines for intensive ecological studies of species belonging to various groups of plants

and animals. Among the outlines on plants are those by Pelton (1951) on trees, shrubs, and stem succulents, by Cooke (1951) on fungi, by Penfound (1952) on herbaceous vascular hydrophytes, and by Stevens and Rock (1952) on herbaceous angiosperms. Since these are so recent, no studies on the ecological requirements and tolerances of a species and based on the outlines have yet appeared. However, in recent years there have been some rather intensive studies on the ecology of certain wild plants. Among the best of these are those by Hall and Penfound (1944) on the American lotus (*Nelumbo lutea*), Jacobs (1947) on the greater duckweed (*Spirodela polyrhiza*), and Penfound and Earle (1948) on the water hyacinth (*Piaropus crassipes*).

In carrying out and interpreting ecological studies of wide-ranging species, it must be remembered that such species may consist of several to many biotypes, each with a slightly different tolerance range. Lawrence (1950) has stressed that the local population of a species should be the basis of work on ecological life histories. These local populations, as Clausen (1951) has pointed out, may consist, depending on pollination factors of a few or many biotypes at any one time. A thorough study of a widely tolerant species, then, would involve working with a number of local strains. This probably would not be necessary with narrow endemics which may consist of only one or a very few biotypes.

Compensation

Among the most interesting plant-environment relations which ecologists have noted is the apparent compensation of one environmental factor for another. This usually occurs near the boundaries of a species' range and allows the individuals of the species to grow in what at first glance does not appear to be a normal habitat. Rübel (1935) has discussed compensation and pointed out that an amount of a factor normally considered limiting for a species can be reduced even farther when compensated for by another factor.

The substitution of elevation for latitude, allowing plants of northern distribution to grow far southward on high mountain ranges, is a well-known example of compensation. A similar situation is brought about by the compensating effect of slope angle and direction for latitude upon northern species on the cooler and moister north-facing slopes, and upon southern species on the warmer and dryer south-facing locations. Cantlon (1950), for example, has shown that north-facing slopes in north-central New Jersey have a vegetation more like that of level areas 300 miles farther north than like that of the south-facing slopes on the other side of the ridge.

Perhaps the most significant types of compensation, from the standpoint of disjunct plant distributions, are those in which parent material apparently compensates for climate. Such compensations are more striking and seemingly more common where certain climatic factors, particularly precipitation and temperature, are low, as for example in cold desert regions. The effects of limestones, serpentines, altered andesites, and other rocks of relatively narrow chemical composition are particularly marked in compensation and endemism.

Limestone often allows certain species to extend farther than normally into cold or wet climates. In Europe, for example, Thurmann (1849) long ago pointed out that certain plants restricted to chalk in northern France occur in the Cevennes to the south on gneiss, a siliceous rock. Shreve (1922) found that in southern Arizona, desert species such as ocotillo (*Fouquieria splendens*) and creosote-bush (*Larrea divaricata*) reach their upper limits from 900 to 1500 feet higher on limestones than on granite. In the Great Basin, there seems to be some tendency for pinyon (*Pinus monophylla*) to extend farther north and to higher elevations on limestones and other rocks rich in calcium. In the central White Mountains of eastern California, dolomites between 10,500 and 11,500 feet are covered with open pure stands of *Pinus aristata* while adjacent quartzite is occupied by a subalpine sagebrush-grass community.

On the other hand, some plants seem to be favored in disjunct distribution by acidic rocks. This seems to be particularly true with species which normally occupy moist montane situations, as a compensation for lesser precipitation when they occur in lower semi-arid regions. For example, several species of Sierran conifers and subalpine herbs extend into sagebrush steppe at some distance from the Sierra Nevada on islands of highly acid and infertile altered andesite (Billings, 1950). Since *Artemisia tridentata* and other desert shrubs and grasses cannot grow on the altered rocks, the soil moisture normally used by them can support the widely scattered conifers. The friable nature of the altered rock also allows deeper root pene-

tration of the trees than would be possible on the neighboring unaltered andesites. It would be interesting to know something of the mineral nutrition of the conifers, compared with the desert plants.

The more the question of parent material compensation is studied, the more it seems to become involved with that of endemism. Almost every rock type allowing compensation also has one or usually more endemic species characteristic of it. This is particularly true of limestones and serpentines, but endemics are present on almost all other chemically unusual rocks also. Mason (1946a, b) has discussed thoroughly and well the relationships between endemism and the highly mineralized nature of the substrates of many endemic plants.

One begins to wonder whether compensation is always an exact compensation or whether it ever is. Perhaps the individuals occupying the unique rock-climate environments belong to unique physiological biotypes. They may in a sense be endemics themselves: "biotypic endemics."

The solution of these complex problems of compensation and endemism lies principally in the use of the methods of experimental ecology, experimental taxonomy, and genetics. An outstanding example of the integrated use of these techniques is that by Clausen, Keck, and Hiesey (1948), who have shown that *Achillea lanulosa* and *Achillea borealis* are each made up of a number of climatic ecological races which react differently when grown in identical environments. Using one of these climatic ecotypes, the Inner Coast Range-Sierran foothill race of *Achillea borealis* (*A. borealis* subsp. *californica* of the Clayton-Knight's Ferry type), Kruckeberg (1951) found that it contained both serpentine-tolerant and serpentine-intolerant edaphic races Kruckeberg correctly argues that since the environment of any particular place is a complex, no single uniform ecotypic response is possible. With this in mind, he has suggested that it might be better to think of natural populations as consisting of continuous or discontinuous arrays of ecotypic variation in response to the sum total of the environmental factors in an area.

Biotic Potential

As Mason (1946a) has pointed out, environment occupies area independently of whether or not a species can grow in that particular environment or be restricted to it. Some species occupy all of the environment which is suited to their ecological tolerances. Other species, because of lack of sufficient time or because of barriers to the ready migration of their seeds or propagules, have not yet occupied all of the environments open to them. Of course, since environments are dynamic and continually changing, some species find their environmental areas getting smaller before they can be filled, while environments open to other species may be expanding.

Man has had a profound effect in altering the biotic potentials of many areas. Where once only the species and genera native to an area had ready access to its various environments, now exotic species from distant but similar environments may be transported and become established there. In some cases, such as that of *Bromus tectorum*, a species seems to be more successful in its new environment than in its native home. Some of this success may be due to gene exchange and evolution among the various ecotypes of the species, since Clausen (1951) has indicated that new ecological races can probably evolve in only a few generations to fit new environmental conditions. According to Stebbins (1950), the biological requirements for such rapid evolution are: (1) a high degree of heterozygosity, (2) a favorable population structure, (3) the degree of potentially preadaptive gene combinations, particularly those related to seeds, and (4) the intrinsic mutation rate. Since many widely distributed weeds are annuals, possibly there has been sufficient time for such genetic change and adaptation to occur simultaneously with their increase in range.

Vegetation Influences

In any discussion of the environment-plant complex, the reciprocal effect of vegetation upon its environment must not be overlooked. Microclimate, soil, and biota are all greatly affected by the structure and changes in the plant cover of an area. The local distributions of many species are greatly influenced by the microenvironments created and maintained by the vegetation itself. Most short-term natural succession is due to the cumulative influence of the principal dominants on the environment. Some of these effects are physical (Billings, 1938) while many are chemical (Went, 1942; Gray and Bonner, 1948). One of the most promising fields in plant ecology is the study of the effects of vegetational types upon the en-

vironment and local plant distribution. Vegetational influences have been given more attention in forestry and range management than elsewhere, as indicated in the excellent compilation and discussion of such effects by Kittredge (1948).

Solution of Complex Environment-Vegetation Problems

As Cain (1944) has said, the exact mathematical solution of complete environmental complex-vegetation problems is extremely difficult, if not impossible. However, with some arbitrary simplification of terms it may be possible to arrive at approximate mathematical answers of great value in the solution of some problems in both applied and pure ecology. Major (1951) has attempted to solve complex vegetation-environment problems by simplifying the environment into five large factors: climate, parent material, organisms, relief, and time. Using these five factors in differential equations in a manner similar to that used with problems in soil formation by Jenny (1941), he has shown how it might be possible to put environment-vegetation relations on a functional, factorial basis.

Major's basic equation, adapted from Jenny, is:

$$v = f\,(cl, p, r, o, t)$$

where v represents any property of vegetation that can be expressed in quantitative terms, and cl, p, r, o, and t represent respectively climate, parent material, relief, organisms, and time. Further adapting the equation to whole plant communities, it becomes:

$$V = f\,(cl, p, r, o, t)$$

where V represents an entire plant community or stand. Since in an assemblage of several species, it is almost impossible to reduce the community quantitatively to a single number, it is not yet possible to use quantitative terms in this last equation. Major follows Jenny in assuming cl, p, r, o, and t to be mathematically independent variables, although he realizes that in nature this is only approximately so. By totally differentiating the first equation, he shows how it is possible to set up quantitative functions of a single variable with all others held approximately constant. For example, a lithofunction would be:

$$v = f(p)_{cl,r,o,t}$$

where parent material varies sharply, with other factors remaining constant. This would be the situation where serpentine adjoins sandstone on the same slope of a hill and the same species occurs in different quantities on the two rock types. Similarly, vegetation could be expressed qualitatively as parent material varies by a litho-sequence:

$$V = f(p)_{cl,r,o,t}$$

Similar equations for functions and sequences of other factors can also be set up.

Major's work is a forward step in the direction of logical expression of vegetational functions and their relations to environment. However, the method should be used with certain concepts borne clearly in mind. The premise that these factors are all independent variables might well cause confusion if the principle of the holocoenotic environment is accepted. Major realizes that these factors are not *ecologically* independent, but makes them *mathematically* independent so that they can be held constant in an equation while a single factor is varied mathematically. This is necessary to evaluate the effect of that one factor on the vegetation or local population. Among the many combinations of environmental factors in nature, examples of different rock types in the same climate can allow an evaluation of the parent material effect. This is only approximate because of the possible effect of parent material on microclimate and other factors, but it is probably close enough for practical results. Also, Major has deliberately restricted his problem to causation between vegetation and environmental factors and has purposely omitted the complex relations between the factors themselves. This, of course, greatly simplifies the problem but creates a more or less unreal situation, since in nature all of these interrelationships ultimately affect plant distribution and vegetation. Some disagreement is to be expected from the choice of only five factors (or groups of factors) to represent the whole environment. This is not too serious, since it would be very easy to add others, such as pyric (i.e., fire), and to set up a pyrofunction for *Bromus tectorum*, for example, in the equation:

$$v = f(py)_{cl,p,r,o,t}$$

Time is very definitely a part of any function or sequence involving vegetation, but whether it is truly an environmental factor is open to ques-

tion. Major concluded, since similar equations can be set up for both vegetation and soil, that they develop concomitantly and that soil formation cannot be separated from vegetative succession. This concomitant development has been clearly shown by the work of Braun-Blanquet and Jenny (1926) and of Pallman, Richard, and Bach (1948), among others.

While most ecological work is still far from the ideal mathematical design proposed above, there is now an increased realization that plant distribution and vegetation are almost always the result of the interaction of several environmental factors. Much careful work, experimentation, and statistical analysis have been done to show the relative effects of combinations of environmental factors upon the growth of certain plants in natural vegetation. Kozlowski (1949), for example, in a thorough study of the growth and competition of oak and pine seedlings, came to the conclusion that the ultimate failure of pine in Piedmont succession is due to *both* low light intensity and decrease in available soil moisture as parts of an environmental complex.

VEGETATION AS AN INDICATOR OF ENVIRONMENT

Since vegetation is the product of the interactions between the environment and the genetic tolerance limits of its component species, theoretically it can be the best indicator of conditions in natural environments. To this end it has long been put to practical use by foresters, range managers, soil conservationists, and farmers. However, certain precautions should be observed in any attempt to describe or to predict changes in an environment from the vegetation present in it.

In the first place, since environment occupies area independently of the plant species present and since many plant species have not yet occupied all of their potential environment, it would be a mistake to evaluate an environment on the basis of the *absence* of a given species. There are many reasons why it might not be present. Environments can better be judged on what species and vegetation are present.

Secondly, while there is some reason for using the physiognomy of vegetation as evidence of the physical environmental conditions, this must be done with great care. Many forests, particularly in western North America, are actually found in drier environments than the grasslands of the Mississippi Valley, but are maintained by a different type of precipitation cycle. Beadle (1951) has pointed out the dangers of assuming that similar climates on different continents will exhibit vegetations of similar physiognomy. Semi-arid climates in New South Wales, for example, are not occupied by grasslands and shrub communities, as they are in North America, but by woodlands of *Eucalyptus*, *Acacia*, *Casuarina*, and other woody plants.

It should always be remembered that each species in a vegetation is distributed according to its own environmental tolerances. The resultant vegetation thus can be used as a delicate indicator of environmental conditions, provided it is analyzed floristically by adequate statistical methods and provided the environmental tolerances and indicator significance of its component species are known. These are difficult to determine on an exact basis and yet an experienced ecologist can, after a quantitative analysis of vegetation with which he is familiar, describe the environment and its cyclic and cumulative changes fairly well. Boyko (1947) has shown how quantitative climatic values can be deduced by using the geo-ecological shifts in environmental amplitudes of certain key species in the vegetation of Israel. However, much more research is needed before these evaluations can be put on an ideal quantitative basis.

As shown by Tüxen and Diemont (1937), Billings (1950), and others, floristic vegetation types within a large climatic type are not the result of climate alone but of the whole environmental complex, in which parent material is just as important as climate. Thus, it must be remembered that vegetation is an indicator of the whole environment and not just of climate, or parent material, or fire, or any other single factor.

CONCLUSIONS

1. The environment of a plant is holocoenotic.
2. Any study of plant growth and distribution in relation to environment must consider each factor in relation to the others of the complex.
3. Factors can be limiting or trigger factors in the dynamic complex. For a given species, these limiting factors may be different in different parts of its range.
4. Environment is dynamic and varies both in space and time.
5. Every plant species is distributed according to its own genetically determined tolerance limits, providing time has been sufficient to allow it to

occupy the whole potential environment open to it.

6. There is a definite need for much more autecological work on tolerance ranges under field or simulated field conditions. The effects of environmental shifts or environmental gradients should be worked out for groups of related species or for the important competing species in a community.

7. One environmental factor may compensate for another and allow a species to exist beyond its apparent tolerance range.

8. Genetic variation within a species, producing ecotypes and biotypes, is probably involved in the question of compensation.

9. It should be possible to put certain environment-vegetation relations on a quantitative functional basis if analyses are well-planned from the standpoint of both vegetation and environment and if enough data are obtained. Some arbitrary simplification of the environment into factors may be necessary to do this.

10. Every plant species is distributed according to the tolerance ranges of its own ecotypes and biotypes. It is independent of other species except where individuals of other species constitute an integral part of its environment. It grows where it does because the *whole* environment in space and time fits its genetic requirements and time and the environment have allowed its seeds or propagules to reach that place. Communities result from such independent distribution and vary gradually or sharply as the whole environment varies.

11. Vegetation can be used as an indicator of total environment if the tolerances of its characteristic species are known and if the vegetation is adequately analyzed by statistical floristic methods.

LIST OF LITERATURE

ALLEE, W. C., and THOMAS PARK. 1939. Concerning ecological principles. *Science*, 89: 166–169.

——,——,O. PARK, A. E. EMERSON, and K. P. SCHMIDT. 1949. *Principles of Animal Ecology*. W. B. Saunders Co., Philadelphia.

BEADLE, N. C. W. 1951. The misuse of climate as an indicator of vegetation and soils. *Ecology*, 32: 343–345.

BILLINGS, W. D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.*, 8: 437–499.

——. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. *Ecology*, 31: 62–74.

BLAISDELL, JAMES P. 1950. Effects of controlled burning on bitterbrush on the upper Snake River Plains. Mimeo. *Intermountain For. & Range Exp. Sta. Res. Paper*, 20.

BOYKO, H. 1947. On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *J. Ecol.*, 35: 138–157.

——. 1949. On climatic extremes as decisive factors for plant distribution. *Palestine J. Bot.*, 7: 41–52.

BRAUN-BLANQUET, J., and H. JENNY. 1926. Vegetationsentwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen. *Neue Denkschr. schweiz. Naturf. Ges.*, 63: 175–349.

CAIN, STANLEY A. 1944. *Foundations of Plant Geography*. Harper & Bros., New York.

CANTLON, JOHN E. 1950. Vegetation and microclimates on north and south slopes of Cushatunk Mountain, New Jersey. Thesis, Rutgers University.

CLAUSEN, JENS. 1951. *Stages in the Evolution of Plant Species*. Cornell Univ. Press, Ithaca, N. Y.

——, DAVID D. KECK, and WILLIAM M. HIESEY. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. *Carnegie Inst. Wash. Pub.* 581.

COOKE, WM. BRIDGE. 1951. Ecological life history. outlines for fungi. *Ecology*, 32: 736–748.

COOPER, WILLIAM S. 1926. The fundamentals of vegetational change. *Ecology*, 7: 391–413.

DAUBENMIRE, R. F. 1947. *Plants and Environment*. John Wiley & Sons, New York.

ERRINGTON, PAUL L. 1939. Reactions of muskrat populations to drought. *Ecology*, 20: 168–186.

GOOD, RONALD. 1931. A theory of plant geography. *New Phytol.*, 30: 149–171.

——. 1947. *The Geography of the Flowering Plants*. Longmans, Green, and Co., London.

GRAY, REED, and JAMES BONNER. 1948. An inhibitor of plant growth from the leaves of *Encelia farinosa*. *Amer. J. Bot.*, 35: 52–57.

HALL, THOMAS F., and WM. T. PENFOUND. 1944. The biology of the American Lotus, *Nelumbo lutea* (Willd.) Pers. *Amer. Midl. Nat.*, 31: 744–758.

JACOBS, DON L. 1947. An ecological life-history of *Spirodela polyrhiza* (Greater Duckweed) with emphasis on the turion phase. *Ecol. Monogr.*, 17: 437–469.

JENNY, HANS. 1941. *Factors of Soil Formation*. McGraw-Hill Book Co., New York.

KITTREDGE, JOSEPH. 1948. *Forest Influences*. McGraw-Hill Book Co., New York.

KOZLOWSKI, THEODORE T. 1949. Light and water

in relation to growth and competition of Piedmont forest tree species. *Ecol. Monogr.*, 19: 207–231.

KRUCKEBERG, ARTHUR R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. *Amer. J. Bot.*, 38: 408–419.

LAWRENCE, DONALD B. 1947. *Experimental Ecology:—Lecture Outline and Laboratory Guide.* Mimeo. Univ. Minn., Minneapolis.

——. 1950. Report of the committee on ecological life histories. *Bull. Ecol. Soc. Amer.*, 31: 25–27.

LIEBIG, J. 1943. *Chemistry in its Application to Agriculture and Physiology.* 3rd ed. Peterson, Philadelphia.

LINDEMAN, RAYMOND L. 1941a. The developmental history of Cedar Creek Bog, Minnesota. *Amer. Midl. Nat.*, 25: 101–112.

——. 1941b. Seasonal food-cycle dynamics in a senescent lake. *Amer. Midl. Nat.*, 26: 636–673.

——. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399–418.

LUNDEGÅRDH, HENRIK. 1949. *Klima und Boden in ihrer Wirkung auf das Pflanzenleben.* 3rd ed. Gustav Fischer, Jena.

MAJOR, JACK. 1951. A functional, factorial approach to plant ecology. *Ecology*, 32: 392–412.

MASON, HERBERT L. 1936. The principles of geographic distribution as applied to floral analysis. *Madroño*, 3: 181–190.

——. 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño*, 8: 209–226.

——. 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. *Madroño*, 8: 241–257.

OOSTING, HENRY J. 1948. *The Study of Plant Communities.* W. H. Freeman and Co., San Francisco.

PALLMAN, H., F. RICHARD, and R. BACH. 1948. Ueber die Zusammenarbeit von Bodenkunde und Pflanzensoziologie. *Sammelb. 10e Cong. intern. Verbandes forstl. Versuchsw.*, Zurich. 57–95.

PELTON, JOHN F. 1951. Outline for ecological life history studies in trees, shrubs, and stem succulents. *Ecology*, 32: 334–343.

PENFOUND, WM. T. 1952. An outline for ecological life histories of herbaceous vascular hydrophytes. *Ecology*, 33: 123–128.

——, and T. T. EARLE. 1948. The biology of the water hyacinth. *Ecol. Monogr.*, 18: 447–472.

PLATT, ROBERT B. 1951. An ecological study of the Mid-Appalachian shale barrens and of the plants endemic to them. *Ecol. Monogr.*, 21: 269–300.

ROBERTSON, JOSEPH H., and C. K. PEARSE. 1945. Artificial reseeding and the closed community. *NW. Sci.*, 19: 58–66.

RÜBEL, E. 1935. The replaceability of ecological factors and the law of the minimum. *Ecology*, 16: 336–341.

SHREVE, FORREST. 1922. Conditions indirectly affecting vertical distribution on desert mountains. *Ecology*, 3: 269–274.

STEBBINS, G. LEDYARD, JR. 1950. *Variation and Evolution in Plants.* Columbia Univ. Press, New York.

STEVENS, O. A., and LEO F. ROCK. 1952. Outline for ecological life history studies of herbaceous plants. *Ecology*, 33: 415–422.

TAYLOR, WALTER P. 1934. Significance of extreme or intermittent conditions in distribution of species and management of natural resources, with a restatement of Liebig's Law of Minimum. *Ecology*, 15: 374–379.

THURMANN, J. 1849. Essai de phytostatique appliqué à la chaine du Jura. Berne. [Cited in Lundegårdh, 1949].

TÜXEN, REINHOLD, and HERBERT DIEMONT. 1937. Klimaxgruppe und Klimaxschwarm. *Jb. Naturh. Ges. Hannover*, 88/89: 73–87.

WENT, F. W. 1942. The dependence of certain annual plants on shrubs in southern California deserts. *Bull. Torrey. Bot. Club.*, 69: 100–114.

RECENT ADVANCES IN OYSTER BIOLOGY

By P. KORRINGA

Government Institute for Fishery Investigations, Bergen-op-Zoom, Holland

INTRODUCTION

A REVIEW of the recent papers dealing with the biology of the oyster is certainly worth-while reading for a public much larger than just those engaged in shellfish work. This, in the first place, is because the word "oyster" figures in the titles of such a very great number of papers that they can be counted by the thousand. Evidently the oyster has attracted more scientific attention than any other marine invertebrate. Moreover, these papers cover a great variety of topics. From this fact one is inclined to conclude that the oyster, biologically speaking, is the best known invertebrate. Nelson (1938) even dares to say that "the oyster is scientifically the best known marine animal in the world." Therefore all students of invertebrate biology and all those interested in the problems of marine ecology may benefit by a review of recent oyster papers, for this may draw their attention to possible gaps in the knowledge of the biology of other invertebrates, and to the influence of thus far poorly understood or even unknown ecological factors.

A review of oyster literature is useful not only because it deals concisely with a great number of papers, but even more because many of these papers are difficult to find, being published in journals with only a small circulation.

In the second place, a review like the present is of value because it leads to the conclusion that in spite of the great number of papers published on the biology of the oyster we do not yet know or understand all about it. On the contrary, the greater the number of papers, the more we feel compelled to admit with complete candor and humility that we have but a poor understanding of many important factors in the oyster's biology, and that marine ecology is a science which is still in its infancy. Recent advances throw doubt on many old certainties, once generally accepted and already firmly anchored in biological textbooks. Perhaps the newly gained insight will usher in a new era of research in marine biology, an era which may ultimately yield a better understanding of the complexity of life in the sea.

The scope of the present review is limited to papers dealing with the biology of oysters. Studies on oyster culture and on other shellfish are left out of consideration, to avoid congestion. To decide which papers should be reckoned among the "recent" contributions is a rather arbitrary matter. Limiting this review to a few years only, might lead to too fragmentary a picture. Taking into consideration that many papers are difficult to trace, and that many others, published during the war years, did not always attract the attention they deserved, I have chosen to include the papers issued since 1940. For the sake of clarity I will occasionally refer to earlier papers.

I. TAXONOMY AND EVOLUTION

A classification of oysters based only on the shape, size, color, and texture of the adult shell has been widely recognized as impossible and unreliable. The enormous range of individual variation in the features of the adult shells, brought about by a variety of ecological conditions, has made many a student despair and has led to complaints like that of Iredale (1939): "Though beloved by gourmets from the earliest time, oysters have never been a delight to systematic conchologists."

It is Ranson who has dared to tackle this intricate problem in our time, and has tried to set up order in this confused field. Too many species and varieties of recent oysters (about 100) and fossil oysters (about 500) had been described too diligently and often on too flimsy grounds. The nature of the substratum (rock, gravel, sand, silt) and other features of the facies, such as salinity, current velocity, wave action, depth, and exposure, may lead to such a variety of shape and texture of the shells that it is certainly absurd to give a name to each such form. Ranson (1943) has also pointed to the fact that large-scale and interna-

tional transplantation of oysters for re-laying has broken the former isolation in Western Europe, so that some old, well defined races of *Ostrea edulis* (like the once famous "Gravette" of the Arcachon Basin, France) have disappeared completely.

Noting the variability of the oyster's adult shell and the enormous influence of the facies, Ranson (1948a) resorted to an approved method, used in the classification of mollusks since Bernard (1898): the study of the features of the larval shell. After a preliminary discussion (Ranson, 1939) of the development and structure of the oyster's larval shell (prodissoconch), and some introductory remarks on the features of the larval shell of *Pycnodonta* (in section 6 of his 1939–1941 paper, and again, this time in greater detail, in his 1942 paper), Ranson came to the point in a paper published in 1948 (Ranson, 1948c). The first larval shell, the early prodissoconch (straight-hinged larva) is of little use in taxonomic studies, since its hinge-part (provinculum) is still undifferentiated. The second phase of the prodissoconch (umbo larva) proved to be very useful in the identification of oysters, since its provinculum shows a characteristic dentition, and since its shape is very constant in each species, though its size may vary somewhat. A great advantage is that the larval shell is not influenced by the substratum. Ranson found that the larval shell can often be detected as part of well-preserved shells of adult oysters, and that moreover very often some spat settles down on the shells of oysters, but perishes soon afterwards, so that tiny larval shells may be found here and there on an adult oyster's shell. In sufficiently large and well-preserved samples of oyster shells, Ranson usually could find some with a persistent larval shell and thus could offer a fool-proof identification of the specimens under consideration. Yet in regions where several species of oysters occur simultaneously, I believe that great care will be required in drawing conclusions from young specimens fixed on the shells of the adult oysters.

This use of the larval shell is the scientific basis of Ranson's work on the revision of recent and fossil oysters, details of which he hopes to publish in the near future. Whenever possible, Ranson uses some characteristics of adult oysters also, e.g., the structure of the "chalky" deposits, so characteristic for oysters, and showing either a foliate or a vacuolar structure; and the presence or absence of the promyal chamber (Ranson, 1950), which separates in some species of oysters most of the right mantle from the visceral mass. It was Nelson (1938) who pointed out the taxonomic value of the promyal chamber, and who mentioned the disproportionate interest in the shell of mollusks as compared with the soft parts. Museum biologists like McLean (1941) are, however, very reluctant to use anatomical characteristics, though recognized as fundamental, and cling to keys based on features of the adult shell only. The greatest care is required, however, in using keys like those of McLean.

Ranson (1948b, 1950) divides the recent oysters into 3 genera:

Pycnodonta. Larval shell with equal valves, 5 teeth equally divided over the provinculum, interior ligament immediately following the provinculum. Anterior to the ligament 10 small teeth on the edge of each valve. Prodissoconch of the right valve not filled in later, but closed up by a vertical calcareous membrane. The empty part of this prodissoconch easily gets lost. This is what led Bernard astray (Ranson, 1942). Adult: oviparous; rectum traverses ventricle; promyal chamber present; "chalky" deposits of vacuolar structure. The latter feature is very characteristic for *Pycnodonta*. Though a definite revision, complete with synonyms, etc., will be given later, Ranson has mentioned in section 6 of his 1939–1941 paper that he checked many recent and fossil *Pycnodonta* for the presence of vacuolar deposits. If such are absent, the species must be transferred to another genus. On the other hand, there are species of oyster which should be named *Pycnodonta* because their "chalky" deposits are of a vacuolar structure. We can add that the oyster described by McLean (1941) as *Ostrea thomasi* n.sp. can thus be easily recognized as a *Pycnodonta* from the photograph on plate 4. The study of the larval shell is necessary to identify the species in this very polymorphic group.

Gryphaea. Larval shell: unequal valves, rather asymmetric, with 2 teeth on each side of the provinculum, interior ligament well away from the provinculum. Adult: oviparous; rectum not through the ventricle; promyal chamber present; "chalky" deposits lamellated.

Ostrea. Larval shell: unequal valves, with 2 teeth on each side of the provinculum, though anterior pair may be reduced, interior ligament placed in the provinculum. Adult: larviparous;

rectum not through ventricle; no promyal chamber; "chalky" deposits lamellated.

Ranson (1950) has added that in some of the members of the genus *Ostrea* (e.g., *O. folium*, *O. glaucina*, *O. crista-galli*) the right mantle is less completely united with the visceral mass than in *O. edulis*, *O. lurida*, etc., but that there is no true promyal chamber in these species. He does not believe that this difference is sufficient to justify splitting up the genus *Ostrea*. Further, he thinks that Nelson (1938) must have made a mistake in saying that the oyster from the Florida mangroves possesses a large promyal chamber. This cannot be *Ostrea frons*, which lacks a promyal chamber, but undoubtedly belongs to the genus *Gryphaea*. According to Gunter (1950), Nelson is now inclined to admit this.

The shape of the prodissoconch shell may serve to identify the species in each genus, which is, in the present state of our knowledge, hardly possible when using the features of the adult oyster only. Following this procedure Ranson reduces the species of recent oysters to 3 *Pycnodonta*, 15 *Gryphaea*, and 20 *Ostrea*. Further investigations, especially cross-breeding experiments, may demonstrate in due time how far Ranson is right in this. However it may turn out, I think there is every reason to follow Ranson in placing all oysters of the type *angulata*, *virginica*, *gigas*, and *commercialis* in a separate genus (which genus should be called *Gryphaea* according to Ranson) and in using the name *Ostrea* for flat oysters only. This will also serve to remind us always that there is a fairly wide gap in many respects between those two groups of oysters, and that we need not worry about finding serious discrepancies in their biological behavior.

In a note, Ranson (1948c) discusses the problem whether of not *Gryphaea angulata* Lmk. may be considered as the type species of the genus *Gryphaea*. He points out that Lamarck's first description of the genus *Gryphaea*, dating from 1801, is but a preliminary one, and that therefore the genus *Gryphaea* should be considered to date from 1819, when Lamarck redescribed it in his *Histoire Naturelle des Animaux sand Vertèbres*. This view accepted, *Gryphaea angulata* Lamarck would be the type of the genus, designated by Children in 1823. Therefore Ranson presented to the International Commission on Zoological Nomenclature at its session held in Paris in 1948 a communication in which he sought to prove that the type species of the genus *Gryphaea* Lamarck is *Gryphaea angulata* Lamarck.

As can be deduced from Hemming's report (1951) in the *Bulletin of Zoological Nomenclature*, a strict application of the international rules of zoological nomenclature leads, however, to the conclusion that the fossil species *Gryphaea arcuata* Lamarck is the type species of the genus *Gryphaea*. Moreover, Children's selection of *Gryphaea angulata* as the type species is invalid since at the time when, in 1801, the generic name *Gryphaea* was first validly published by Lamarck, the name *Gryphaea angulata*, then cited by Lamarck, was a mere *nomen nudum* and accordingly does not rank as an originally included species, and is ineligible for selection by a later author to be the type species of the genus in question.

Therefore Gunter (1950) is certainly right in having stated that a strict application of the international rules of nomenclature leads to using the generic name *Gryphaea* for some fossil species only (type species *G. arcuata*), and to the conclusion that the generic name *Crassostrea* (Sacco, 1897) is the first valid name for oysters of the type *angulata*, *virginica*, *gigas*, etc. Gunter has rightly stressed that these oysters differ in too many respects from the flat oysters to lump them with the latter under the generic name *Ostrea*.

However right Gunter may be, I feel very reluctant to use the generic name *Crassostrea* and to suppress the genus *Gryphaea* for recent species. This would certainly enhance the confusion. For, up till now, very few have ever used the name *Crassostrea* for the Portuguese oyster and its nearest allies, while the term *Gryphaea* has been used very widely in this sense, even among practical oystermen. It is the feeling of others also that too strict an application of the "rules" often leads to absurdities. Fortunately, there is a way to get around such difficulties: the plenary powers of the International Commission on Nomenclature could be used to suppress the name *Gryphaea* Lamarck, 1801, and all uses of that generic name from 1801 to the date of 1819, when it was republished by Lamarck in the *Histoire Naturelle des Animaux sans Vertèbres*. Then the name *Gryphaea* Lamarck 1819, thus validated, has as its type species the recent species *Gryphaea angulata* Lamarck, 1819 (by selection by Children, 1823). This is stated in the note by Hemming, the object of which is to attract the attention of interested specialists to the problem.

Awaiting the final decision of the International Commission on Nomenclature, I have to make a preliminary choice for the present purposes. To minimize confusion I prefer to follow Ranson, and will therefore use in the present paper the very familiar name *Gryphaea* for all oysters of the type *angulata*, *virginica*, *gigas*, etc. In any case I agree completely with both Ranson and Gunter that these oysters should be placed in a separate genus.

In this difficult nomenclatural matter I have been kindly advised by Dr. C. O. van Regteren Altena of the Leyden Museum of Natural History. Maybe a greater number of interested specialists, until now not familiar with Hemming's report, will furnish the Commission on International Nomenclature upon its request with their view on this important and intricate problem, so that the confusion may eventually be cleared up.

Ranson (1949a) published a note on three Lamarckian oyster species: 1) Lamarck's *Ostrea deformis*, on which Ranson found some larval shells, should be named *O. dolabriformis* Philippi (Martens); 2) Lamarck's *Ostrea numisma* is in fact a *Pycnodonta*, as its vacuolar "chalky" deposits demonstrate; 3) Lamarck's *Ostrea margaritacea*, sometimes named *O. iridescens* or *O. procellosa*, of which Ranson investigated the original specimens, should be named *Gryphaea margaritacea* (Lmk).

Ranson is continuing his investigations and indicates that he has found larval shells in at least some well-preserved fossil oysters, which will greatly facilitate their revision.

In his 1943 book *La Vie des Huîtres*, (of which an unrevised and completely identical copy appeared in 1951 under the title *Les Huîtres, Biologie, Culture* from a different publisher, without even mentioning the earlier edition), Ranson enunciated his ideas about the evolution of the oysters. I wonder whether many professional evolutionists will accept his views, which are as follows.

Many species of oysters are known from the Cretaceous period, but the recent species did not appear before early in the Quaternary. Since then no evolution has taken place in this group. The *Exogyra* from the Cretaceous led to the *Gryphaea*. Most Cretaceous oysters, among which the genus *Ostrea* already figures, lived in deeper water with high salinities. Only later did oysters, with the exception of the genus *Pycnodonta*, begin to inhabit coastal waters. According to Ranson, it is absurd to assume that deepwater species migrated to coastal waters with reduced salinities, since that necessitates profound modifications of the protoplasmic reactions. Most probably recent species came from those few which possibly already lived in coastal waters in the Cretaceous.

Ranson claims that new species only come into being during the transition between two geological periods, during which the entire fauna is renewed. At the end of a geological period a new species may arise by sudden mutation and at the cost of another species, which then disappears completely. Mutations in our time never overstep the boundaries of the species. There is now no progressive differentiation leading to new varieties and species. The creation of a new species by mutation is not a local event, but happens simultaneously all over the world. Quite unknown cosmical factors are no doubt involved in the process. Ranson gives as example *Pycnodonta squarrosa*, which lived all over the world in the Neogene and was replaced completely at the beginning of the Quarternary by *P. hyotis*, which since then also occurs all over the world. Ranson claims that the chromosomes are not involved in mutations which lead to new species, but that such mutations, happening only during transitions of geological periods, should be conceived as changes in the molecular network of the protoplasmic proteins.

Personally, I like Ranson's unravelling of taxonomic puzzles with the aid of the features of the oyster's larval shell better than his highly speculative conceptions of evolution in oysters and other living beings.

II. ANATOMY

Nelson (1938), in dealing with the oyster's promyal chamber, clearly demonstrated that our knowledge of the anatomical features of the oyster's soft parts is far from complete. I know only one recent paper devoted to the oyster's anatomy, viz., the study of Nelson and Yonge (1947) on the early development of the gills in the American Atlantic oyster (*Gryphaea virginica*). The short description given of the development and functioning of the young gill in recently metamorphosed oyster spat does not lend support to the classical phylogenetic concept of "ascending" and "descending" gill filaments. A continuous functional food groove, which is said to aid in early respiration too, appeared to be present in a very early stage, which would be impossible according to the classic theoretical view, which holds that the filaments elongate.

If, however, we insert in this section studies on the shell structure, we can also point to the following contributions: Ranson (1940c) has described some noteworthy details of the hinge of the oyster shell. After metamorphosis the oyster's hinge has no longer any dentition, but only a ligament. A special highly vascular tissue secretes the ligament. This tissue consists of a thicker central part and two thinner lateral parts, so that the ligamental area of the shell shows a deeper central part ("fossette") and two shallow lateral parts ("bourrelets"). This is the case in both shells in the genus *Ostrea*, but in the cupped valve only in oysters of the *Gryphaea* type. The ligamental area of the flat valve in the latter shows a higher, instead of a deeper, central part. The thicker central part of the ligament is often called the resilium (cf. McLean, 1941). As the oldest part of the ligament is steadily destroyed by microorganisms (unlike most other bivalves) the oyster is forced to go on secreting new ligamental material. In doing this the central part of the ligament becomes broader and broader, and thus gets its typical trapeziform shape. The rotting away of the ligament leads to the typical "beak" present in older oysters, especially in those which live in the mud.

In his next paper, Ranson (1941a) claims that the vacuolar layers in the shell of *Pycnodonta* are secreted by the mantle's outer margin (bourrelet marginal) only. If *Pycnodonta*'s vacuolar layers are, however, to be compared with the "chalky" deposits in *Ostrea* and *Gryphaea*, the entire mantle epithelium will have the faculty of secreting either vacuolar or harder layers.

In his 1939–1941 paper Ranson dealt with the structure of the shell in the oyster. Though I can confirm most of his observations, I cannot agree with many of his deductions and theories, as I stated earlier in a paper on the "chalky" deposits in the shell of *Ostrea edulis* (Korringa, 1951a). This shell consists of a periostracum, extremely thin and hyaline and therefore often overlooked, a prismatic layer on the flat valve only as imbricate brown scales, and the calcite ostracum, which forms by far the greater part of the shell. The calcite ostracum consists of harder subnacreous layers and of the so-called "chalky" deposits. The latter are of a very porous structure, as Ranson demonstrated in detail (1939–1941). Their cavities contain sea water; or in dry museum shells, air and sea salts. Apart from those salts there is chemically very little difference between the harder and softer parts of the calcite-ostracum. The "chalky" deposits are slightly richer in organic material than the hard subnacreous layers. The elastic scales of the prismatic layer, however, contain much more organic material (about 4 per cent). Orton's hypothesis that "chalky" deposits are secreted where the mantle becomes detached from the shell is to be rejected. If the mantle becomes detached from the shell (e.g., through shrinkage during rapidly increasing salinity), water-filled pockets are formed in the shell ("chambrage"). Neither could I accept Ranson's opinion that ample "chalky" deposits are secreted only where the substratum is rich in lime. I believe that the oyster does not take in the calcium it needs for constructing its shell with its food in some particulate form, but as calcium ions, so plentiful in the surrounding sea water. I adduced evidence that the oyster uses "chalky" deposits as a measure of economy in smoothing out the inner surface of the shell. In depositing "chalky" layers it requires only one-fifth as much material (both organic and inorganic) as it would need in constructing the same volume of shell of the hard subnacreous layers. Very extensive "chalky" deposits are to be found opposite the exhalent chamber of *Ostrea edulis* beyond the muscle scar. It could be demonstrated that the oyster keeps the distance between both valves at that place limited to about 0.5 to 0.6 cm. The more the oyster is cupped, the more extensive the "chalky" layers at that place. Presumably this has some bearing on the oyster's efficiency in functioning. I want to stress here that the features described are characteristic for *Ostrea edulis*, and probably for other oysters of the flat type. *Gryphaea* oysters do use "chalky" deposits in smoothing out the shell interior, particularly in distorted shells, but usually lack the heavy layers opposite the exhalent chamber. I presume that this could be explained by the fact that in *Gryphaea* most of the water drawn through the gills leaves through the promyal chamber, instead of through the exhalent chamber. Thus ample "chalky" deposits are unnecessary, and the adductor muscle can be placed closer to the shell margin, which increases its efficiency in functioning, as Nelson (1938) rightly remarked.

Independent of Ranson, Medcof (1944a)—whose work I did not know at the time I wrote my own study on *Ostrea edulis*—gave a detailed description of the porous structure of the "chalky" deposits in *Gryphaea virginica*. He rightly stated that "chalky" deposits are used in smoothing out

the shell's interior surface, that "they help to maintain certain topographical features of the shell interior, preserve a size relationship between meats and shell cavity and regulate the curvature of the inner face of the shell throughout the oyster's life." "Chalky" deposits are laid down in the summer season and are covered later with harder layers. This holds good for *Ostrea edulis* too. Medcof found very extensive "chalky" layers in oysters from a station in the Bras d'Or lakes (Nova Scotia). These oysters were in very poor condition and finally "became the poorest of all oysters examined." Medcof suggested that the need which those poor oysters must experience for economy of shell-building materials is the probable cause for extensive secretions of "chalky" rather than pearly shell. It would, however, be more economical still to omit all shell growth and thickening under such conditions. I therefore wish to put forward the view that in the oysters of the Bras d'Or lake the shell cavity gradually becomes too large for the shrinking body. The oysters, always wanting to maintain contact between mantle and shell, narrow down their shell cavity by ample secretion of the economic "chalky" layers.

Galtsoff, Chipman, Engle, and Calderwood (1947) also found copious "chalky" deposits in shells of poor oysters in the York River (Va.), for which the same explanation could be advanced. They gave, moreover, some details on the shell structure, which, however, had been previously described.

III. CHEMICAL COMPOSITION

Oysters and other Lamellibranch molluscs may accumulate considerable quantities of the metals Al, Fe, Cu, Zn, and Pb. This is especially remarkable when the small amounts of these metals which usually occur in sea water are considered. Galtsoff (1941, 1942) demonstrated that manganese also may be present in the oyster's tissues in noteworthy quantities. In analysing samples taken over a long period at biweekly intervals, he found in winter 7–11 mg. of Mn per kg. dry weight in the oyster's tissues, and in summer as much as 35–55 mg. per kg. dry weight. This seasonal difference is real, since it cannot be explained by differences in the intestinal content. High figures were found for ovary and gills. In the adductor muscle the quantities of manganese and the seasonal differences are small. After spawning a marked drop in the manganese content is noted, but this happens with many other of the oyster's chemical components.

Galtsoff assumed that the seasonal fluctuations indicate that manganese has a physiological significance in the oyster, perhaps as a catalyst in the storage and utilization of glycogen. He announced experimental studies in this field, but we have not heard about the results thus far. In my view seasonal changes in manganese content, and in the quantities present of the metals mentioned above, are not necessarily correlated with a greater physiological demand for these elements in certain parts of the year. During feeding the oyster probably cannot avoid collecting and ingesting those ions which adhere firmly to the mucous feeding sheets. Collecting them is less of a problem to the oyster than getting rid of them. Only gradually does the oyster manage to excrete those products again. Therefore, in periods of active feeding (summer season) a considerable accumulation may take place. The gills especially show a considerable seasonal variation, much more so than the adductor muscle, which is less involved in the metabolic process. Usually much metal is accumulated in leucocytes and is therefore found in the highly vascular parts of the connective tissues around the digestive gland. Excessive quantities of copper are known to endanger the well-being of the oyster, as well as its consumer. In our experiments we found that the oyster also accumulates Hg ions, when administered in very low concentrations, and that if it cannot get rid of that metal quickly enough, so much is accumulated that it gradually leads to the oyster's death. Accumulation of such elements during the summer season therefore does not necessarily mean that these elements are of physiological importance to the oyster—in any case not in the quantities observed.

Several recent studies are devoted to the seasonal fluctuations in certain chemical components of the oyster's body. The important reserve food glycogen has attracted especial attention. Efforts were made to improve the chemical methods of determining glycogen in oysters (Humphrey, 1941; Calderwood and Armstrong, 1941). Hatanaka (1940), working with *Gryphaea gigas*, found a considerable drop in the content of glycogen per individual oyster in the season of reproduction. But protein and fat also showed a considerable decrease in summer, though not precisely simultaneous with that of glycogen. As even ash and water content decreased in the reproductive season, we conclude that the entire body of the oyster must have diminished considerably. Though all the different components show an increase in the

autumn months, they all lag far behind the figures found before spawning started. This is abnormal. After complete recovery from spawning the old prespawning weight should be surpassed. It is difficult to judge, however, in how far Hatanaka's individual oysters are perfectly comparable, since he failed to inform us about the exact size and the volume of the shell cavity in his oysters. The importance of the volume of the shell cavity for the sake of comparison is rightly stressed by Medcof and Needler (1941), and later also by Ingle (1949). Hatanaka has also given tables of the chemical components expressed in percentages per gram dry weight, figures which show quite a different trend. Thus expressed, glycogen appeared to remain fairly constant throughout the year. In the mantle margin it even showed the highest amount during the summer. In the gonad tissues it did decrease drastically in summer, which automatically gives an increase in the percentage of protein per gram dry weight. Such figures show that these methods do not readily lead to a good understanding of what is really going on in the oyster's tissues in the course of the year.

The same holds good for the work of Humphrey (1941b), who worked with the Australian oyster, *Gryphaea commercialis*. He first tells us that good condition in an oyster means that the meat has a creamy color and fills the shell cavity completely. He does not agree with the general opinion that "fat" oysters are necessarily rich in glycogen. For, shortly before spawning, when the oyster is "ripe and running," its condition is excellent, although the glycogen reserve may be very small at that time. From a purely biological point of view Humphrey is right, the oyster then is in perfect condition. But when we speak about the condition of an oyster, we mean as a rule its quality as a marketable oyster—and oysters full of spawn certainly are not attractive for the discriminating consumer. Humphrey next pointed to the fact that there is a considerable variation among duplicates in glycogen determinations, which can be ascribed to individual differences in the rate of sexual development, perhaps also to nutritional conditions, the presence of parasites, etc. That the yearly course of glycogen in his samples of oysters is quite smooth could partly be ascribed to the incomplete homogeneity of his samples. Each individual oyster shows quite different figures in the course of the year. Where Humphrey's samples were taken, the season of spawning may be of long duration, so that all phases may occur simultaneously in the samples. In one of his graphs Humphrey compared the percentage of glycogen with the oyster's wet meat weight and seemed very much surprised that the latter hardly drops during the spawning period, while glycogen goes steeply down. This brings Humphrey to the conclusion that glycogen must be converted into or replaced by some other substance, which has not yet been identified. That the wet meat weight does hardly drop is certainly a surprise, since so much material leaves the oyster as eggs and sperm. It casts doubt on the reliability of his sampling. Large scale overlapping of developmental phases may have obscured the real events. Some of the lost material may, however, have been replaced by water. Data on the dry meat weight would have been interesting here.

It is further noteworthy that Humphrey stated that his oysters did not lose any glycogen during storage in air. Even if the storage was continued for 20 days, the glycogen figures were scarcely influenced.

Gaarder and Alvsaker (1941) certainly have been very unfortunate in their work. They started a painstaking and time-consuming series of analyses of samples from a batch of oysters (*Ostrea edulis*) placed on suspended trays in one of the Norwegian oyster polls. These polls are well-sheltered ponds which have a communication with a fjord. In some the communication is temporarily cut off, which leads to high water temperatures in summer, so that spat production can take place there. In the other polls marketable oysters are grown. Not only did these workers determine the content of glycogen, fat, proteins, and water, but also ash, C, P, S, Cu, Fe, Zn, K, Na, Mg, Ca, Cl, and sometimes also F, Br and I. This certainly was a tremendous work and it is therefore highly regrettable that the biological knowledge gained is hardly worth mentioning. Sampling was begun in September, 1935, and ended in April, 1937, when the supply of oysters was exhausted. As the authors were seeking for correlations between chemical composition and sex change, they would have included two, instead of one, season of reproduction for the same amount of work, had they started sampling in March, 1936. The only season of reproduction covered (1936) was unfortunately most aberrant. First, it appeared that practically all the oysters had hibernated as advanced females, which is most unusual. As a rule, the advanced stages of both sexes form a minority in winter. Therefore, male individuals appeared only later in the summer

season, often after having spawned as females earlier, whereas only simultaneous sampling of male and female oysters living under exactly the same conditions can lead to trustworthy results about fundamental differences in their chemical processes. The worst, however, was that the investigators hit a very unfavorable autumn in 1936, with so little sunlight that food production was not only unsatisfactory, but was even so limited that the batch of experimental oysters placed in a poll for spat production (Selvågpol) in April, 1936, starved to death. Those oysters which remained in the original poll (Ytrepoll) did slightly better and escaped death from starvation, but their condition was unsatisfactory and proper recovery after spawning did not occur. Therefore the results of the elaborate chemical analyses can hardly give us a general insight into the chemical changes during a normal season of reproduction. It is certainly possible that the female phase makes higher demands upon the oyster's food reserves than the male, but the figures of Gaarder and Alvsaker do not suffice to bear out their tentative conclusion that the male phase is characterized by a fundamentally different type of metabolism (changes in proteins and ash) from the female phase (glycogen and fats). The investigators also found a much higher meat weight in oysters hibernating as females than in those wintering as males, and stated that the latter have only a poor chance of survival. This made Gaarder remark later (1950) that consumers prefer female oysters because they are fatter. This cannot be generally true. At least in Holland and France the oysters do not hibernate in advanced phases of sexual development, and the general condition in large batches of oysters in very uniformly good in winter, the season for marketing oysters. It is noteworthy that in the work of Gaarder and Alvsaker the steep drop shown by many of the figures during the spawning period clearly demonstrates the high demands made by egg and sperm production. Calculations per oyster are certainly more interesting than percentages per gram oyster meat—either wet or dry—since by the latter method a considerable change in one of the categories automatically brings about reciprocal changes in the other percentages, which would wrongly suggest material changes in the latter categories. In giving figures per oyster, indications of the volume of the shell cavity may help to reduce the influence of individual variations in size (information which is not given by Gaarder and Alvsaker). It is also interesting to note the observed accumulation of metals like Fe, Cu, and Zn in early summer. The galvanized wire of the trays may have influenced the figures for zinc. The ratio N:P was shown to be 9:1 as in marine plankton, and the ratio C:N:P was 100:16.5:1.85, as in other marine organic matter.

IV. HISTOCHEMICAL STUDIES

Far more interesting information on changes in the oyster's chemical components and their biological background can be obtained with histochemical methods. Such work was undertaken by Mlle Bargeton (now Mme Couteaux). For glycogen studies she preserved her material in alcoholic Bouin saturated with picric acid (to prevent the dissolving of glycogen), made serial sections, and stained these for glycogen with iodine, Best's carmine, and with chromic acid following the Bauer method. As a control, saliva-treated sections were used. For histochemical studies of other components other methods of fixation and staining were employed.

In her first paper, Bargeton (1941) noted that the typical glycogen-bearing connective tissue of the oyster in which the so-called cells of Leydig predominate (120 x 20 μ when rich in glycogen, 30 x 10 μ when poor in glycogen) occurs in several other places in the animal kingdom. Thus *Lumbricus* (Oligochaeta) shows a similar specialized glycogen distribution. It stores its glycogen in a tissue histologically almost identical with the oyster's cells of Leydig. In the oyster these cells may be completely full of glycogen in the autumn.

Bargeton (1942) next dealt with the prespawning changes observed in biweekly samples taken from February to July, 1941, of Portuguese oysters (*Gryphaea angulata*) living on the coast of the Isle of Oléron (France). In winter, glycogen was abundant in the oyster. High concentrations were found in the perigastric tissues, in a layer of connective tissue encircling the intestines, and also in the mantle and labial palps. The main body of glycogen is, however, stored in the interstitial connective tissues of the gonad. The genital follicles are greatly reduced then. Bargeton observed a severe decrease in the glycogen content as early as March, before the gonad started differentiating. The connective tissues around the gonad became lighter, with larger meshes. Later in March the gonad started proliferating, and female oysters were full of oogonia by mid-April. Glycogen accumulated rapidly in the Leydig cells at that time,

but the proliferating gonad soon superseded the connective tissues. There was no direct correlation between changes in glycogen and the development of the gonad follicles. In the perigastric tissues the glycogen content did not change materially. In April, during rapid gonad development, glycogen was accumulated here, and also in the mantle and around blood vessels. Bargeton noted that the 1940–1941 winter was unusually severe and that the Portuguese oysters apparently suffered a great deal in early spring. It remains doubtful, therefore, whether it is normal for glycogen to decrease greatly in March and for only the glycogen freshly accumulated after resumption of feeding to serve as reserve food during gonad development. Control series taken in years with a normal winter would elucidate this.

Very interesting are Bargeton's (1943) observations on the same oysters during spawning and in the post-spawning period. Genital products fill the gonad tissue almost completely just prior to spawning, but only here and there does one see a piece of the walls of the genital follicle. There is extensive fusion of the genital follicles in both females and males. The walls of the genital follicles lose their continuity and only a few small islets of connective tissue are found around a blood vessel. After spawning the genital follicles individualize very rapidly. Muscle fibers and collagen fibers form a coat around the genital epithelium and thus lead to a rapid closing of the temporary holes. Immediately the connective tissues gain ground again, big Leydig cells filling rapidly with glycogen, and smaller cells appearing in great number. Some eggs and some sperm may remain after spawning. As a rule these are expelled later in the season. Bargeton also observed a resorption (earlier observed in *G. commercialis* by Roughley) in which a very dense interfollicular tissue develops around the remaining spawn. Most probably this is an accumulation of phagocytes giving the impression of a tissue of polyhedric cells, because they are so crowded.

Bargeton's 1944 paper deals with fat reserves in the Portuguese oyster, *Gryphaea angulata*. Fat certainly is not negligible in oysters, although glycogen is the main storage product. The fat content increases rapidly during gametogenesis. Much fat is accumulated in the eggs. After spawning the fat is more uniformly distributed over the oyster's body. Details of the whereabouts of fat in the cells of the connective tissue are given. There is no antagonism between glycogen and fat. The highest fat content was, indeed, found in an oyster with as much as 13½ per cent of the fresh weight as glycogen. In the digestive gland, fat is localized in the acini, in the high and clear cells. No fat was found in the smaller darker cells, which may be younger. The fat content was found to vary from 0.7 per cent to 2 per cent of the fresh weight. After a cold winter the fat content decreased considerably. The fat in the connective tissue is used during gametogenesis, the fat in the cells of the digestive gland is not.

An old problem is next solved by Bargeton (1945). As already indicated concisely in her 1941 paper, glycogen in the digestive gland is not to be found in the acini themselves, but only in the interstitial connective tissues. Her histochemical methods demonstrated that the interstitial cells may be very rich in glycogen (up to 16 per cent), but that they are not numerous enough to give the entire digestive gland a high glycogen content by the usual chemical analysis. *Ostrea edulis* appeared to have more glycogen-bearing connective tissue among the acini of the digestive gland than *Gryphaea angulata*. In an ordinary chemical analysis parts of the tissues surrounding the stomach and intestine, which are rich in glycogen, are difficult to eliminate completely.

More details on glycogen in *Gryphaea angulata* are given later (Couteaux née Bargeton, 1947). General feeding conditions and gametogenesis determine the glycogen content. As a rule *Gryphaea* is said to be poorer in glycogen than *Ostrea*. Oysters rich in glycogen look thick and creamy. A maximum is observed in winter (November–January). A rapid decrease in glycogen may be found in early spring, which gives the connective tissue a spongy appearance. As remarked above, the decrease in *Gryphaea* in early spring may, or may not, occur after a normal winter, and this, we hope, will be ascertained in due course. Only scanty histochemical information is available on *Ostrea edulis* and other oysters. Serious loss in glycogen in early spring is not recorded for these oysters. Though I agree that on the market the Portuguese oysters are often leaner than the flat oysters, I do not believe that this is because *Gryphaea* does not fatten so well as *Ostrea edulis*. If placed in waters rich in food *Gryphaea* may fatten so much that they nearly become too plump to eat. Such oysters certainly will beat the fattest *Ostrea edulis* in glycogen content. It is further noteworthy that Bargeton's investigations never led to the finding of fundamental differences in

male and female oysters, which is contrary to Gaarder's view.

Histochemical investigations like those carried through by Bargeton not only give detailed information on the whereabouts of certain chemical components in the body of the oyster, and their seasonal fluctuations, but they also give a prompt answer to all questions regarding sexual development, spawning, parasites, etc. In the ordinary chemical analyses such inquiry is not only as a rule impossible, but through the pooling of the individual oysters of each sample most of the real fluctuations may be greatly obscured. Therefore elaboration of the histochemical techniques, and also for products other than glycogen and fat, may lead to a better understanding of what really goes on in the oyster in the course of the year.

V. BIOCHEMISTRY

Humphrey has contributed most to the knowledge of the biochemical processes of the oyster's tissues. In the glycolytic system of the adductor muscle of *Gryphaea commercialis* Humphrey (1943b) demonstrated that phosphate, K, Mg, or Mn and diphosphopyridine nucleotides are essential. Oyster glycogen, and also rabbit glycogen and starch, but not fructose, glucose, galactose, or mannose, can act as a substrate for the reaction. Pyruvic and lactic acids are produced in glycolysis. Fluoride and iodoacetate inhibit the acid production.

The presence of catalase was demonstrated in several organ systems of the oyster (Humphrey, 1943a). The method used was based on the decomposition of H_2O_2. In the controls addition of 0.1 ml. of 0.1 M NaCN prevented the action of the catalase. The gonad always appeared to be richest in catalase, closely followed by the digestive gland. The optimum pH appeared to be 6.7, but the results at a pH of 7.0 hardly differed. 15° and 25°C. gave high figures. At 35°C. a great diminution of the reaction was observed.

Later (1946) Humphrey described his investigations on the endogenous respiration of a homogenate of the adductor muscle of *Gryphaea commercialis*. He measured the oxygen uptake of his preparation. Na and K salts accelerated, and Ca and Mg salts inhibited the respiration. The Q_{O_2} of the homogenate was −0.21.

The succinoxidase system in the muscle homogenate (Humphrey, 1947) was also studied by measuring the oxygen uptake. Little was known at the time about the function of C_4-dicarboxylic acids in invertebrates. Cyanide appeared to be a powerful inhibitor; methylene blue, on the other hand, increased the oxygen uptake. Humphrey agreed with Maloeuf that the oyster can be classified as an animal with no respiratory pigment. The presence of hemocyanin or other oxygen transporters could not be demonstrated in the oyster's blood. Humphrey added that the oyster has only a very small concentration of cytochrome or cytochrome precursor, which is demonstrated by the strong inhibitory effect of cyanide. The stimulating influence of methylene blue confirms the absence of an oxygen carrier. The oyster's muscle appeared to possess a very active system for the metabolism of succinate, but Humphrey concluded that the oyster as a whole has a low metabolism.

The effect of several narcotics on the endogenous respiration and the succinate oxidation in a homogenate of oyster muscle was discussed by Humphrey in 1948. Though the results differed quantitatively from those obtained with vertebrate muscle, Humphrey did not believe that the part played by succinic acid is fundamentally different in the oyster. Many narcotics reduced oxygen consumption in concentrations ranging from 0.0001 to 0.05 M. Oxidation of succinic acid was partially inhibited by these concentrations of the narcotics used.

Other information of a biochemical nature will be discussed in the sections on anaerobic life, egg development, and spawning.

VI. RESPIRATION

Galtsoff and Chipman (1946) measured oxygen consumption and CO_2-production in *Gryphaea virginica*. To obtain data corresponding to the level of basal metabolism, their experimental oysters were first starved for 24 hours. The experiments were carried through at a constant temperature of 25°C. The average value of the R.Q. varied from 0.80 to 1.05, but showed no definite trend which could be associated with the season, sex, or condition of the oysters. A general decline in oxygen consumption was, however, noticed in both sexes after spawning. This post-spawning decrease is tentatively ascribed to loss of weight and reduced activity of adductor muscle and ciliated epithelium.

According to E. Pedersen (1947), it is the oyster's mantle, with its highly ramified vascular system, which is charged with the respiratory function. In her experiments she placed oysters (*Ostrea edulis*) in well stoppered 2 l. glass jars,

which were then hung out under water in the two basins of the Flødevigen hatchery (Norway) in which her stock of oysters lived. Thus the factors of temperature and light did not differ during the experiments from those prevailing among her oysters previously. To avoid errors the shells were carefully cleaned and covered with enamel. Moreover, every oyster was packed in a gauze bag during the experiments in order to ensure that small shell fragments which might break off while turning and handling the jars, were included in the analysis. Measuring the uptake of oxygen met with little difficulty, but estimation of carbon dioxide required special precautions, for organic acids may also be present in sea water. The oyster does excrete measurable quantities of organic acids (e.g., lactic acid) when kept in jars with unfiltered sea water. These acids free CO_2 from the oyster's shell. The production of organic acids was found to be greatly reduced if the oysters were kept in filtered sea water before and during the experiments. Though all organisms under 5 μ and some of slightly greater dimensions passed the filter-paper, the oysters produced no feces in filtered water. This is a second advantage, since errors through oxygen uptake by feces are thus avoided. In jars with filtered water the oxygen uptake corresponded very well with the carbon dioxide production, the R.Q. ranging from 0.9 to 1.0 in every season. At low water temperatures very little oxygen is used by the oyster. At 0°C. the quantity is hardly measurable. At 5°C. about 2 cc./100 g. total wt. oyster (shell included)/24 hrs. is used; at 10°C., 5 cc.; at 15°C., about 10 cc.; at 20°C., 20 cc., and at 25°C., about 30 cc. Miss Pedersen observed that individual oysters may demonstrate considerable differences in this respect, which she ascribes to different living intensities: "Enkelte individer kan har en forskjellig livsintensitet."

Changes in temperature, both increases and decreases, reduce the oxygen consumption considerably. After some time (3 days are enough as a rule) the oyster becomes accustomed to the new temperature and uses normal quantities of oxygen. In one of the basins used supersaturation with oxygen up to 300 per cent did occur for some time, without affecting the oyster's respiration. Filtration of such water did, however, reduce oxygen to the 100 per cent saturation level, so that experiments in the jars with filtered, oxygen-supersaturated water was impossible. The sudden transition from 300 per cent to 100 per cent oxygen did reduce the oyster's respiration temporarily, but changes in oxygen tension of smaller amplitude and below 100 per cent) had no perceptible effect. It is interesting to note Miss Pedersen's finding that the oyster can live for quite a while in water poor in oxygen (the limitations for the oyster's well-being have not been studied), and appears able to use practically all the available free oxygen.

I wonder whether the small organisms passing the filter-paper would not produce conditions of supersaturation in the jars if these were immersed for a few days before introducing the experimental oysters. I further doubt whether Miss Pedersen is right in assuming imperfect circulation inside the jars, since the oyster's own pumping brings about considerable water movement. The necessity and effect of turning the jars at intervals have not been demonstrated. It is preferable to avoid all unnecessary disturbance during the experiments.

VII. ANAEROBIC LIFE

As soon as the oyster closes its shell tightly, be it under water or when exposed to air, many processes come temporarily to a standstill (e.g., digestion). Still, even a dormant stage requires some metabolism, which is carried on anaerobically in a closed oyster. Dugal (1939), who earlier studied the anaerobic metabolism in *Venus mercenaria*, found there a type of glycolysis comparable to anaerobic glycolysis in vertebrates. Non-volatile organic acids are produced, but the $CaCO_3$ of the shell has such a buffering effect that the pH in the mantle cavity hardly changes. The organic acids free carbon dioxide from the calcium carbonate of the shell, and this makes the CO_2 content of the mantle cavity increase from about 6 to 150 vols. per cent in *Venus*. All this CO_2 comes from the shell and none directly from anaerobic glycolysis.

Dugal (1940) assumed a similar procedure in the oyster (*Gryphaea virginica*), viz., a transformation of glycogen into a weak non-volatile organic acid which is neutralized by the calcium carbonate of the shell. He presumed that anaerobic metabolism in the oyster can last as long as glycogen reserves are available, and tried to prolong the oyster's life out of water by injecting glucose. It is interesting to remember here that Humphrey (1943b) stated that glucose cannot act as a substrate for the glycolytic process in the oyster's adductor muscle (cf. section Biochemistry). The paper by Dugal (1940) being an abstract only, and no further details having been published since, we cannot find out to what extent

injections with glucose had a perceptible effect on the length of time *Gryphaea virginica* can live out of water. Neither do we know whether his controls received injections without glucose, to avoid errors caused by differences in moisture.

Dugal and Fortier (1941) stated later that the calcium content in the oyster's mantle cavity increases from 40 to 400 mg./100 cc. during exposure to air, and that this is accompanied by a commensurate increase in carbon dioxide content. The weak non-volatile organic acid produced by the oyster during anaerobic glycolysis is not, contrary to expectation, lactic acid. Its quantity added to the CO_2 produced from the shell was found to be equivalent to the calcium content in the mantle cavity.

Though the oyster's anaerobic metabolism will reduce the glycogen supply, I wonder whether a serious reduction in glycogen (i.e., in "fatness") of the oyster does readily result from exposure to air. We have noted above the observation by Humphrey (1941b) that his oysters (*Gryphaea commercialis*) did not lose any glycogen during storage in the air up to 20 days at room temperature. Nor have we ever heard or experienced that oysters kept out of water soon lose their "fatness." I cannot believe that the eventual death of an oyster when exposed to air is usually caused by exhaustion of its glycogen supply ("jusqu'à ce que la réserve en glycogène du foie soit épuisé"—Dugal, 1940). Loss of moisture certainly is an important factor, too. It is noteworthy that *Gryphaea virginica*, when properly packed and kept at temperatures slightly above the freezing point, can be kept out of water and retain most of its fatness for several months (Needler, 1941a). Baker, Boyd, Clarke, & Romano (1941) analysed at intervals of 2 to 4 weeks oysters stored at 4°C. and 100 per cent humidity. During the first two months of storage no appreciable changes occurred in the content of water, glycogen, lipids, or iodine. During the third month, however, the water content decreased by 2½ per cent, the glycogen content by 37 per cent, and the iodine content by 18 per cent, but the phospholipid content increased by 65 per cent! It is not known exactly what processes lead to these changes, but it is certainly remarkable that there is such a sudden decline of glycogen in the third month of storage. That storage at a slightly higher temperature greatly reduces the oyster's life out of water (Needler, 1941a), does indicate that some metabolic process may be the limiting factor. We do not know to what extent oxygen and carbon dioxide in the air exert an influence during the oyster's life out of water. Oysters of the genus *Ostrea* are less hardy in this respect than *Gryphaea*. At low temperatures *Ostrea edulis* can stand at most 24 days of exposure and live. Complete recovery is still possible after 18 days of exposure. More information about the oyster's anaerobic life would be very welcome indeed.

VIII. FEEDING

The nutrition of the oyster, though one of the basic problems of oyster culture, is only partially understood. Detailed studies were earlier devoted to the intricate coordinated ciliary action of the oyster's gills, which drives a current of water through the ostia (gill slits). During this passage particulate matter can be filtered off and, wrapped in mucus, it is then transported to the labial palps, where it is decided whether the food will be ingested, or rejected as pseudofeces. It is usually assumed that objects too large or too spiny are refused. The oyster, thus being considered as a kind of living submarine vacuum cleaner, may indeed be found to have a great variety of material in its stomach. Thus Cerruti (1941) has recorded as stomach contents of *Ostrea edulis* grown in the Mar Piccolo (Italy) among large quantities of organic detritus, diatoms and flagellates, larvae of annelids, sand, silt, spicules of sponges, larvae of molluscs, eggs and gastrulae of a variety of marine invertebrates, plant fibers, pollen grains, and smuts from the nearby marine wharf. Nelson (1947) has assumed that the number of marine bacteria ingested by oysters may be very great indeed, since detritus particles may be literally covered with bacteria. About 40 per cent of the products of decomposition are said to be incorporated into bacterial protoplasm. It has been demonstrated earlier that oysters can capture particles as small as bacteria.

In the greenish or brownish contents of the oyster's stomach diatoms are readily recognized and identified, and this is one of the main reasons why diatoms are often reckoned among the oyster's most important foods. Nelson (1947) has recorded that large numbers of *Skeletonema costatum* could be found in the oyster's stomach during a period when this diatom flourished, and he is therefore inclined to consider *Skeletonema costatum* as the most valuable of all diatoms.

How the oyster manages to filter off not only diatoms and other "large" objects, but also bac-

teria and small flagellates that may easily slip through the ostia, which are from 30 to 60 μ wide while functioning, has been hard to understand. It was MacGinitie (1941, 1945) who solved this problem. He demonstrated that the cilia of a bivalve gill serve to create the water current through the gill, but that they do not themselves strain the food from the water, as had been thought for a long time. It is true that in experiments large carmine particles, which cannot pass the gill slits, are moved by ciliary action along the gill filaments to the edges of the gills, and thence to the labial palps. But in filtering off such small particles as bacteria and the like quite a different technique is used. The mollusc then produces sheets of mucus, and it is these mucous sheets which strain out small particles of food from the water. The frontal cilia move the mucous feeding sheets to the labial palps. Careful observation showed that the small food particles caught in the mucus do not follow the grooves between the gill filaments, but are deflected anteriorly, taking a more oblique path to the oyster's mouth. Oysters and other bivalves react to a variety of disturbing factors by stopping the secretion of the mucous sheets, so that actual feeding is interrupted for shorter or longer periods. The gills may, however, go on pumping water. It therefore should never be said that a bivalve is feeding just because it is maintaining a current through the mantle cavity. Investigations with *Urechis* (Echiuroidea) taught MacGinitie that even particles between 36 Å and 90 Å in diameter may be caught by mucous feeding sheets comparable to those in use by bivalves, some gastropods, and tunicates. Unfortunately no dye has yet been found to stain the pure mucus of a feeding sheet in the living animal, a discovery which would greatly facilitate further observations. MacGinitie was greatly impressed by the efficiency of mucus as a net for straining food from the water. On an earlier occasion (Korringa, 1949a) I indicated that MacGinitie's findings might throw new light on many controversies and paradoxes in the oyster's nutrition. There is now ample evidence that oysters and other bivalves feed partially, if not indeed largely, on very small food particles. It has moreover repeatedly been observed that such small particles are sometimes filtered off almost quantitatively, while at other times they pass unhindered through the gills of the very same oyster. We now understand that the presence or absence of a mucous feeding sheet during pumping was probably responsible for the difference observed.

Closer investigation of the mucous feeding sheets and their efficiency is desirable. By far the greater part of the organic matter present in coastal sea water is usually assumed to be "dissolved" organic matter, because it passes a Berkefeld filter. In the Oosterschelde (Holland), about 10 to 15 per cent of the organic matter is located in organisms and particles measuring over 5 μ, and a further 10 to 12 per cent is of smaller size but does not pass a Berkefeld filter. The remainder does pass, but part of it is probably not in true solution but truly particulate in nature, and perhaps some of that may be caught by a mucous feeding sheet. MacGinitie stresses the importance of the size of the mesh in such feeding sheets, but I think it possible that the electrical properties of both food particles and feeding sheets also determine whether or not particles are readily caught. In this respect it is interesting to note that positive polyvalent ions like Al^{+++}, Cu^{++}, Fe^{++}, Zn^{++}, Hg^{++}, and Mn^{++} are very easily caught and accumulated by the oyster, but not positive monovalent ions like Na^{+} and K^{+} (though present in greater quantities), or negatively charged ions. In using dyes great care is required, since the dye itself may be easily caught by the mucus, and this could lead to disputable conclusions about the size of mesh in the feeding sheets.

According to the observations of MacGinitie, the formation of the feeding sheets is the most sensitive process in bivalve feeding, being more readily disturbed than the rest of the feeding mechanism, such as the pumping of water through the gills. Therefore, a closer study of the feeding sheets should be included in those investigations undertaken to find out whether or not certain conditions are injurious to oysters. This is not necessary if the quantity of food present in the oyster's stomach is used as the criterion whether or not active feeding has taken place, as in the studies of Loosanoff and Nomejko (1946b) with *Gryphaea virginica*. Having determined that the oyster's food passes the entire intestinal tract in 80 to 150 minutes at the prevailing water temperature (20°C.), Loosanoff and Nomejko took samples of oysters at regular intervals. Their experimental oysters did not stop feeding at any phase of the tidal cycle nor at any time of day or night. About 80 per cent showed well-filled stomachs in every sample. Individual variations largely predominated

over possible influences of tides and hour of the day. Laboratory investigations demonstrated that the rate of pumping was the same with water collected at different stages of the tidal cycle. Each oyster pumped from 5 to 25 l./hr., but for shorter periods the rate of pumping in *Gryphaea virginica* could reach 31 to 34 l./hr., this being about 1500 times its own meat weight per hour. The experimental oysters kept their shells open for 94.3 per cent of the 24 hours. Oysters fixed on a platform in opposite directions, thus either facing the tidal current or getting it from behind, showed no difference in their feeding. The authors rightly concluded that in the stations used (Long Island Sound and Milford Harbor, Conn.) feeding is not limited to any part of the tidal cycle nor to any time of day or night.

This has been corroborated by Chestnut (1946) for one of his stations in Delaware Bay. In this station, where a high and fairly constant salinity prevailed throughout the tidal cycle, the oysters appeared to feed at any time. In stations higher up the river a period of low salinity could be observed round about low tide. There the oysters appeared to stop feeding so long as the low salinities prevailed. Wherever low salinities occurred temporarily there was found to be a uniform response to the decrease in salinity, with a complete cessation of feeding activities. Chestnut concluded that Nelson's earlier assumption that oysters do not feed during the ebb tide is right only when the word "ebb" is replaced by "low tide" and for places where the salinity fluctuates considerably in the course of the tidal cycle.

Several studies are devoted to the effect of factors other than salinity on the oyster's rate of pumping.

It is obvious that water temperature greatly influences the volume of water oysters pump through their gills. Loosanoff (1950a) found that only insignificant quantities were pumped by *Gryphaea virginica* at very low temperatures (below 3°C.). From 8° to 16° the pumping appeared to increase rapidly. It is surprising that no changes worth mentioning occurred between 16° and 28°. From 28° to 32° the rate of pumping increased again, reaching maximum figures within this range (37 l./hr. of sustained pumping; up to 40 l./hr. for periods of 5 to 15 mins.). Above 34°C. the oysters began to show distress, resulting in a marked decrease in the rate of pumping and in abnormal shell movements. It is interesting to note that oysters transferred from 3° to 20° began pumping at the same rate as control oysters which were kept steadily at 20°. Loosanoff is certainly right in stating that *Gryphaea virginica* demonstrates a very rapid adjustment to such temperature changes.

In studying factors which are presumably injurious to oysters, one should always realize that the formation of mucous feeding sheets is probably more readily disturbed than the rate of pumping. Therefore, the finding of a normal rate of pumping does not prove that the experimental conditions do not affect the oyster's feeding activities. Loosanoff and Tommers (1947) found that low pH values, which may occur naturally by an influx of acid swamp water or by industrial pollution, reduce the oyster's rate of pumping. At a pH of 7.75 the oyster appeared to pump normally. From pH 6.75 to 7.00 the oyster pumped more vigorously than the control oysters during the first few hours, then fell behind them. At pH 6.5, the rate of pumping was low from the beginning of the experiment, and at pH 4.14 a decrease to 10 per cent of the normal pumping rate was measured. The effect of silt and some other turbidity-creating substances on the rate of pumping has been described in a second paper by Loosanoff and Tommers (1948). Even quantities as low as 0.1 g. per liter of sea water did seriously reduce the rate of pumping (to 40 per cent of the normal value). If 1.0 g. was added per liter the pumping rate fell to 20 per cent, and if 3 or 4 g. were administered per liter of sea water, only 4 per cent of the normal quantity of water was pumped through the gills of the experimental oysters (*Gryphaea virginica*). The substances tested (natural silt, kaolin, chalk) gave comparable results. The oysters expelled large quantities of the suspended materials in the form of pseudofeces. Vigorous shell movements were associated with the frequent ejections of large quantities of material accumulated on the gills. When the oysters were returned to clean sea water, the normal rate of pumping was soon resumed. The authors consider it possible that experimenting with oysters which are used to a life in rather turbid water might yield figures differing from those quoted. Some of the turbidity-creating material was found in the stomach. Conclusions on the ingestion of turbidity-creating substances should, however, be drawn with the greatest caution. In our own experiments we found that the mussel (*Mytilus edulis*) does

filter off suspended chalk or carbo adsorbens if administered in various concentrations. When placed in small glass jars (3 l.) all the material strained off is deposited as pseudofeces. In larger containers (200–500 l.), containing the same number of mussels and the same concentrations of solids as the small jars, the mussels ingested most of the solids and produced but little, if any, pseudofeces. Though this seems hard to explain, it has repeatedly been observed, and it may be that oysters too show some differences in their feeding behavior if placed in larger volumes of water.

Very interesting are the findings of Loosanoff and Engle (1947a, b) that the rate of pumping may be influenced by the density of microorganisms present in the water. In these experiments, too the volume of water pumped through individual oysters was measured. As noted above, it is not justifiable to identify this with the intensity of the oyster's feeding, when one is not sure that all the food is strained from the water during its passage through the gills. The investigators—at that time not familiar with MacGinitie's work—were very much surprised to find that great variations occurred in their experiments in the percentage of cells retained by the gills. When feeding with a *Chlorella* suspension, the oysters retained from 0 to 92 per cent of the cells. The percentage filtered off fluctuated considerably and irregularly, and apparently there was no correlation with the concentration of the organisms administered. These observations clearly demonstrate that pumping and feeding are not identical in the oyster. In efforts to fatten oysters artificially the authors had often observed weak and lean oysters with empty stomachs in the midst of dense plankton cultures. In laboratory experiments they found that there are rather definite concentrations above which the density of microorganisms begins to interfere with the rate of pumping in the oyster (*Gryphaea virginica*). Not only did the rate of pumping decrease, but the oysters also became sluggish in response to stimuli, as if some toxic product had exerted an influence. Dangerous quantities were 3000/ml. for *Euglena*, 75,000/ml. for the smaller *Nitzschia closterium*, and 2,000,000/ml. for the very small *Chlorella* sp. Transferred to normal sea water, the oysters resumed their normal rate of pumping after some time. The observations cannot be explained by simple clogging of the gills with consequent suffocation, since the very same phenomenon was observed when the plankton organisms themselves were eliminated by passing the cultures through a Berkefeld filter. It is concluded that certain inhibiting substances must be present in the dense plankton cultures, most probably metabolic products of the microorganisms under consideration. These products were found to be heat-resistant and aeration did not reduce their toxicity. If the rate of pumping was reduced, it was observed that the quantities of pseudofeces produced were roughly proportional to the concentrations of plankton. True feces showed a reverse relationship. With the aid of these findings a tentative explanation was given by Loosanoff and Engle (1947a) for some cases of poor oysters in waters very rich in plankton (e.g., in Great South Bay, where up to 3,000,000 small green algae were counted per ml. of water). To defend the view that plankton may be toxic when present in too dense masses, the authors mention some cases of "red tides." Kincaid (1951) has noted that such a "red tide," caused by extreme abundance of *Gonyaulax*, may occasionally lead to serious losses among oysters (*Gryphaea gigas*) on the beds in the Northern part of Willapa Bay (Wash.). I believe that "red tide" is only an extreme case of a very widespread and normal phenomenon, the production of metabolic excretions—some of which may be poisonous if present in high concentrations—by living organisms. Plant ecologists can already identify the chemical nature of some of these excretions, which may inhibit the germination and growth of other plant species, but marine biologists lag somewhat behind in this and only now begin to admit hesitatingly that metabolic excretions, especially those produced by microorganisms, may be of ecological importance. I feel sure that it is not the number nor the volume of microorganisms which is decisive in determining the level dangerous for other organisms (such as oysters and their larvae), but that it will be found in due course that certain species do produce great quantities of toxic products, while other, perhaps closely related species are quite harmless. In the experiments described above we should consider that the toxic excretions may be produced either by the plankton organisms themselves, or by the bacteria which abound in such dense cultures and live on the organic excretions produced by the plankton organisms. A wide and most interesting field of investigation here awaits further exploration. It is desirable not only to learn the effect of the metabolites of the many different microorganisms upon other

living beings, especially upon those in which man has an interest, but if possible also to learn more about the chemical nature of such metabolites, in order to detect their presence and to measure their concentration in natural waters, as well as in the laboratory.

That besides chemical products that inhibit the oyster's feeding other substances may occur naturally in sea water which promote the oyster's rate of pumping, has been found by Collier, Ray, and Magnitzky (1950), while working at Pensacola (Florida). During their extensive series of observations on shell movements and the rate of pumping in individual oysters (*Gryphaea virginica*), using an intricate and self-registering apparatus, they observed a correlation between pumping and a hitherto unreported factor naturally present in small amounts in sea water. This factor has tentatively been designated a carbohydrate, since it can be measured photometrically with the N-ethyl-carbazole reagent. It may be a true carbohydrate or it may be some other component which happens to be quantitatively associated with the carbohydrate responding to the test. It passes a bacteriological filter and cannot be removed by centrifugation. It is not destroyed by boiling, but if sea water is stored at 25° to 30°C. its quantity drops sharply after 4 days. Though some individual fluctuations occurred, the oyster (*G. virginica*) stopped pumping when less than 4.8 mg./l. of the carbohydrate was present in natural sea water. At higher temperatures (28°C.) the threshold value may be as high as 12 mg./l. The more carbohydrate, the more vigorously the experimental oysters pumped. Up to 25 mg./l. (arabinose equivalent) was found in the natural sea water at Pensacola. The water which had passed the gills of the oyster under the experimental conditions appeared to have lost from 5 to 15 per cent of its carbohydrate content. Salinity variations of reasonable amplitude did not interfere with this phenomenon. In water with too low a concentration of the carbohydrate factor (and possibly poor in adequate food) the oyster does not feed at all. It then takes from time to time a sample of the water in which it is bathed and closes its shell again after such a test if the required threshold quantity of carbohydrate is not exceeded. Here we meet again the fascinating problem of "dissolved" organic matter in sea water. Evidently bacteria cannot break it down completely. The greater the surface area of particulate matter which may serve them as a base of operations, the better bacteria can lower the level of dissolved organic matter, according to ZoBell and his coworkers. This may explain the steep drop in carbohydrate content after a few days storage of sea water in glass containers, as mentioned above. Though Collier, Ray, and Magnitzky consider the quantities found to be "minute," calculations make us wonder whether their computations are correct. If we take, for instance, the Basin of the Oosterschelde with its 600,000,000 m^3 of water, and if this water contains 10 mg./l. of dissolved carbohydrate (calculated as arabinose), which is a very conservative figure for the Pensacola waters according to Collier, this amounts to as much as 6,000,000 kg. of carbohydrate. It will be interesting to obtain information on the carbohydrate content of other coastal waters, and also of oceanic waters. Immense quantities of organic matter may form a dead or almost dead reserve there. Here we wonder again how much of it can be caught in some way or other by a variety of invertebrates, which brings us to the old, much-disputed problem once raised by Pütter.

Though the paper of Collier et al. is only a preliminary note, and more detailed information can be anticipated, it is desirable to be well aware of the possible effect of this so far unknown factor upon oysters, and perhaps upon other invertebrates, and to take the greatest care in drawing general conclusions from observations on the rate of pumping and the rate of feeding under artificial conditions.

It has often been thought that oysters, in selecting their food, do not discriminate between different types of microorganisms and reject as pseudofeces only those objects which are found to be of unsuitable size or shape. Yonge (1946) rightly noted that small particles of many kinds, including silt and small sand grains, are imbedded in mucus and passed on to the mouth, quite irrespective of their food value. Loosanoff (1949a) published some very interesting observations which clearly demonstrate that the discriminating power of the oyster's labial palps is not limited to the factor's size and shape. Yeast cells are refused and rejected, while plankton organisms of the same size and shape, mixed with the yeast cells, are readily ingested. Loosanoff fed his oysters successfully with a dilute suspension of a mixed plankton culture. If, however, he mixed in a little of a culture of the red *Chromatium perty*—which measures only 2 to 3 μ—these red cells were selectively thrown out as pseudofeces, while the bulk of the

plankton mixture, green-brown in color, was normally ingested by the oyster. If I had not seen with my own eyes in Dr. Loosanoff's laboratory that his oysters, feeding from a mixed plankton diet, did eject red pseudofeces which upon closer investigation appeared to consist of a practically pure culture of the red *Chromatium*, I would hesitate to admit that the oyster's palps are capable of such efficient discrimination. Though the details of the mechanism are still unknown, we can provisionally assume with Loosanoff that the oyster's palps probably possess specialized cells which act as chemoreceptors. They can ensure that unwanted organisms, probably recognized by the nature of their secretions, are duly refused. The oyster does ingest many an indigestible particle and organism, but actually refuses organisms which it presumably recognizes as inimical.

All this clearly demonstrates that the oyster's feeding is a much more intricate and delicate process than is generally supposed and that the comparison with a vacuum cleaner is absurd.

IX. DIGESTION

The view of Yonge (1946) that apart from the action of the style enzymatic digestion is practically exclusively intracellular in lamellibranchs, and that the digestive diverticula are the site of intracellular digestion and absorption, is generally accepted among shellfish biologists. The prevalence of intracellular digestion in lamellibranch molluscs has, however, recently been questioned. Mansour (1946a) found rapidly disintegrating zooplankton in the stomach of a freshly caught *Tridacna*, and assumed that extracellular enzymes produced by the mollusc itself accounted for this disintegration. The digestive gland was thought to secrete both proteolytic and lipolytic enzymes because chlorophyll injected into the foot of *Unio* found its way to the lumen of the intestine as green-brown globules issuing from the digestive gland. Yonge (1946) replied that though true extracellular protease and lipase are lacking in the gut of lamellibranchs, phagocytic blood cells loaded with powerful enzymes may pass in great number into the lumen. He adduced evidence that this may lead to the digestion of fat globules by their becoming surrounded by these phagocytes. Though Yonge can scarcely visualize phagocytes as secreting, he assumes that some may burst and thus liberate their enzymes. Possibly the presence of zooplankton in stomach and gut stimulates phagocyte migration. Mrs. Mansour née Bek (1946, 1948) carried through laboratory experiments in which she tested filtered amoebocyte-free stomach juice of *Tridacna* and *Pinctada* for the presence of proteolytic and lipolytic enzymes. She recorded positive results, but was not yet sure of the origin of the enzymes. Mansour-Bek assumes that secretion globules arising from the digestive gland are involved, but the influence of burst phagocytes cannot be excluded. She admitted that the strength of the enzymes, as indicated by the results of her experiments, does not correspond to the quick disintegration of zooplankton in the stomach of *Tridacna* recorded by Mansour. This is the more marked since all her experiments lasted 24 hours, while the time the food needs for passage through the mollusc's entire intestinal tract is at most a few hours at the high water temperatures prevailing in Egypt, where the Mansours work. There is as yet no proof that Mansour's observations preclude other explanations than digestion by the mollusc's own extracellular enzymes.

Perhaps the investigations on feeding and digestion in molluscs with the aid of radioisotopes, which are now being carried out (Anon., 1950) in the Beaufort Fisheries Laboratory (N. C.), will ultimately bring more certainty. For, since it is possible to follow the metabolism of tagged compounds of various elements in the animal body, the radioisotopes are very important research tools in physiology.

Several authors have observed that at least part of the food ingested by the oyster passes through the entire intestinal tract undigested, sometimes even alive. Nelson (1947) has claimed that at least the smaller diatom species are digested, for he often found the empty frustules in the oyster's stomach. He admits that ingestion does not necessarily imply digestion, but rightly adds, "nor does the presence of living plankton forms in the feces of any animal necessarily mean that such organisms are incapable of being digested." Loosanoff and Engle (1947a) observed that *Chlorella* and *Nitzschia* may leave the oyster's rectum in such good condition that new plankton cultures can easily be started with them.

Cerruti's observations (1941) are very interesting. Only very small diatoms are reduced to empty frustules in the oyster's intestinal tract, but larger forms (e.g., *Coscinodiscus*, *Pleurosigma*) emerge from the oyster unchanged and often alive ("Tutte o quasi tutte le diatomee più minute e sottile erano ridotto ai puri frustuli"). We

wonder whether the digestible diatoms are so small that they can be digested intracellularly by the oyster's phagocytes. Many other objects, e.g., algal spores, leave the oyster's gut unchanged. Lamellibranch larvae, oyster larvae included, are often ingested in great numbers. They always leave the oyster alive. Cerruti clearly demonstrated that these larvae very rarely succeed in freeing themselves from the mucus and organic detritus they are wrapped in, and therefore are doomed to perish ("In ogni caso grandi quantitá di essi trovano, in questo curioso fenomeno, la fine"). The same holds good for *Mytilus* and *Tapes*. It is noteworthy that in *Venus verrucosa* the oyster larvae in the feces appeared to be dead, though practically undigested.

The feeding method of lamellibranchs certainly is very wasteful. Only part of the material ingested can be digested. Many organisms, including their own larvae, find an untimely and useless death, being smothered in the feces which are often deposited in the mud.

X. FATTENING

It goes without saying that both growth and fattening are important problems in the oyster industry and therefore deserve the attention of shellfish biologists. Oysters which have reached a marketable size gain in quality and thereby in price as greater quantities of reserve food are accumulated in their tissues. Oysters rich in glycogen and consequently with meats thick and creamy in appearance are designated as "fat."

We agree with Needler (1941a) that there must be enough food for the oyster to grow and fatten well, and that though little is yet known about this, the food supply is evidently insufficient in some areas. We have seen, however, in earlier sections that Loosanoff and Engle (1947a) demonstrated that we are not justified in saying that any conditions, which result in an increase in the numbers of food organisms in the water will make for fatter and better oysters. Generally speaking, we can say that three factors predominate in the fattening of oysters, viz., fluctuations in quantity of available food, variations in the oyster's intensity of feeding, and interference by the using up of considerable quantities of reserve food in spawning.

Poorly informed as we still are about what really constitutes the most suitable food for the oyster, we unfortunately have no methods of measuring the quantity of available food in samples of water. We do know that considerable fluctuations may occur and that increases in the fertility of the water often lead to fatter oysters. The fertility of the coastal waters is usually governed by the influx of fresh water, which brings nutrients, some of which are leached away from the fields by the rain. We are therefore not surprised that Nelson (1941b, 1947) found leaner oysters after dry periods and fat oysters after floods. Nelson found that oysters fattened rapidly after the South Jersey flood of September, 1940, and observed a flourishing of *Skeletonema costatum* at that time. The plankton net catches, however, only the larger forms, and the possibility remains that nanno-plankton organisms, bacteria, and organic detritus showed a peak too in the very same period, so that we are not justified in concluding with Nelson that it really is only *Skeletonema costatum* on which the oysters fattened. Nelson also claimed that especially the bog-iron, brought down by the river, stimulates the growth of diatoms. Considering the well-known stimulating effect of soil extract on the growth of plankton organisms, we do not feel sure that iron is the dominating factor in this.

In some waters growth and fattening stop in mid-summer, and this is often ascribed to the loss of reserve products by spawning. In waters rich in nutrients we may, however, observe a continuation of growth throughout the summer season and fattening alone is there temporarily interrupted by the oyster's spawning activities. This is the case in the Oosterschelde. In the past, a very dense population of oysters in this district repeatedly led to a wholesale interruption of growth and insufficient fattening (Korringa, 1947a), presumably as a result of an insufficient food supply. According to Hopkins (1946), the experience of the Pacific coast oyster growers was similar, for they consistently noted that with increased quantities of seed planted (*Gryphaea gigas*) growth and fattening became much slower. Hopkins rightly concluded that there is a limitation on the number of oysters which any piece of ground or body of water can nourish and support. Imai, Hatanaka, Sato, and Sakai (1951) record that growth and fattening of *Gryphaea gigas* in Mangoku-Ura inlet (Miyagi Prefecture, Japan) is very poor indeed whenever too many oysters are relaid there. Lambert (1950) recorded a continuous growth of oysters in the French "claires" (fattening ponds), which are rich in nutrients, and claimed to have obtained positive results by administering fertilizer (30 kg. of super-phosphate

per hectare). Rochford (1951) felt reason to believe that in at least some Australian estuaries the microbiota in the superficial layers of the tidal mud flats form the initial section of a food chain for the growing and fattening of oysters. He tried to fertilize such mud flats with a mixture of superphosphate and linseed oil meal and claimed that oysters (*Gryphaea commercialis*) placed in trays above such enriched plots grew and fattened better than his control oysters. We hope that further experiments will reveal the relation between the quantity of fertilizer used and the actual increase in size and condition of a well-defined number of oysters, so that it can be deduced whether or not this procedure is attractive from a practical point of view.

Even in waters rich in food the oysters are usually leanest immediately after spawning. Gunter (1942), who obtained some data on the yield in gallons of oyster meat per barrel of oysters fished on the natural beds in Texas, is probably right in ascribing the poor condition of these oysters in October mainly to the fact that the oysters finished spawning as late as September. After that their condition improved gradually (active feeding going on all winter in the waters of the Texas coast) to reach a maximum in February and March. To what extent a flourishing of plankton in the winter season is involved in this increase in condition, is still uncertain.

Interesting is the observation by Halewyck and Leloup (1951) that the Portuguese oyster (*Gryphaea angulata*) may grow and fatten well, while the European flat oyster (*Ostrea edulis*), living in the very same limited body of water, does not. The authors suggested that growth and fattening of *Ostrea edulis* might be improved by reducing the salinity, but I do not believe that there is yet sufficient evidence to support that view, for *Ostrea edulis* often does grow and fatten very well in waters of much higher salinity. I demonstrated earlier (Korringa, 1950) that neither is it certain that intraspecific competition interfered with fattening of *Ostrea edulis* in the experiments mentioned above.

Medcof and Needler (1941) studied the influence of temperature and salinity on the fattening of oysters (*Gryphaea virginica*). A good comparison was possible by using the "index of condition" computed by dividing the weight of the dried meat, expressed in grams, by the volume of the shell cavity. Thus the influence of differences in size of the individual oysters is practically eliminated. As might be expected from the greatly reduced physiological activity of the oyster at low temperatures, little change was observed under 5°C. If the temperature rises, the oyster's condition first declines, presumably because feeding is insufficient to offset catabolism, but as soon as the 15°C. level is surpassed the condition improves rapidly. Above 20°C. spawning takes place, which brings about a sharp drop in the stored reserve foods. This is later followed by recuperation, especially after the temperature drops below 20°C., so that no further spawning will take place. The authors are right in stating that the relation of the oyster's condition to temperature may be explained on a basis of the balance between anabolism and catabolism. From the data presented it can be concluded that the range from 15°C. to 5°C. is not necessarily accompanied by a noticeable decline in condition in the autumn. In stations where low salinities prevail (under 20‰) fattening may be very unsatisfactory. Presumably the oyster's feeding activities are so much reduced by the low salinity there, that insufficient quantities of food are collected to offset catabolism. Perhaps the quantity of available food also differed noticeably in these stations.

Medcof (1944b, 1946a) made an interesting experimental study on the effect of relaying and transferring on the fattening of oysters. Relaying here means the replanting of oysters on the same bed from which they are fished, and transferring, replanting upon another bed. It is a general experience in the oyster districts of Prince Edward Island (Canada) that the oyster (*Gryphaea virginica*) reproduces well in the warmer waters upriver, but shows better growth and fattening in the colder and often somewhat more saline waters downriver. Experimental relaying and transferring at regular intervals (May 8, May 20, June 9, June 26, July 28, Sept. 1, Oct. 11, Nov. 9) allowed analysis of the phenomenon. To avoid interference by differences in salinity, up- and down-river beds of equal salinity were selected. The above-mentioned index of condition was again used to compare the oysters. Fat oysters had an index of 120 and higher, medium oysters of about 100, and lean oysters of 85 and less. Additional samples were taken from untouched oysters on both the up-river and down-river beds. Relaying of oysters led to an increase in condition of about 10 per cent compared with the untouched oysters. A maximal effect was attained if the relaying was carried out shortly before the period of autumn

fattening started. This phenomenon is explained by the fact that oysters sit higher on the bottom after relaying and thereby enjoy a better internal and external circulation. Accordingly the differences are smaller on harder beds, where the oysters always sit higher on the bottom. Transferring had no appreciable effect if carried through after termination of the autumn fattening. Earlier transplantations clearly demonstrated that conditions for autumn fattening are decidedly better down-river than up. Down-river the oysters are much fatter and show a slighter individual variation. Only during a short period in spring, when the water warms more rapidly up-river, do the oysters living there enjoy a temporary start. Salinities being practically equal (25–29‰), Medcof stated that so far there is nothing to indicate which factors, other than water temperature, are involved. Differences in quantity of available food may exist, but so far are not measurable. As we have seen in earlier sections, there may be several factors other than water temperature which affect the oyster's rate of feeding.

It is interesting to find (Medcof) that oysters transferred early from poor to rich water do better than those which lived all the time in richer water, while on the contrary oysters transferred early from richer to poorer water lag behind those which always live in the poorer water. This is in accordance with our own experience in Western Europe: oysters brought from poor to rich water usually grow and fatten very well, often better than the local oysters. This phenomenon clearly indicates that factors other than water temperature alone are involved in Medcof's experiments.

Further analysis of the conditions affecting fattening, especially variations in food content and fluctuations in feeding intensity, are required to increase our knowledge of this important matter, so that we may ultimately learn how to control the fattening of oysters in limited bodies of water.

XI. GROWTH

By growth one usually understands increase in the size of the oyster's shell. The oyster enlarges its shell by depositing shell material. But not all shell secretion is designated as growth, for most investigators use the term growth only to indicate increase in diameter of the shell, and not for shell thickening. Though the thickening of both the newly made and older parts of the shell is certainly as important to the oyster as the making of new shoot, it has so far received very little attention, since it is difficult to observe and measure in the living oyster.

Without doubt shell growth is correlated with the growth of the oyster's living tissues. If the oyster does not feed or is in poor condition, it will not enlarge its shell. At most it may then repair possible damage, which repair is often erroneously considered as growth. Ranson (1949b) assumes that growth of the living tissues precedes all shell growth ("L'huître qui accroit sa coquille en largueur et longueur est une huître dont la masse des tissues s'est accrue antérieurement"), so that growth of the shell in spring has been preceded by growth of the tissues in winter, and shell growth in the autumn by tissue growth in summer. He has rightly stated that the relation between shell growth and tissue growth is still obscure. Personally I believe that the correlation between tissue growth and shell growth is much closer than Ranson assumes. I do not believe in alternation of prolonged periods of tissue growth with periods of shell growth in the oyster, but suppose that both may occur practically simultaneously, and, under favorable nutritional conditions, continually.

Just how the oyster increases its shell in length, breadth, and thickness is only partially understood. Shell secretion means deposition of both some organic material (conchyolin) and large quantities of calcium carbonate, but this not necessarily by the same cells or glands. Bevelander and Benzer (1948), working with marine bivalves other than oysters, assumed that the conchyolin ("fibrous organic membrane") is formed by the cells of the mantle epithelium, which are described as being of cuboidal to tall columnar shape, and that calcium is secreted by "mucus" glands, which occur in great numbers between the epithelial cells. These glands were found to give a positive test for calcium phosphate. This is my view for oysters too. The epithelial cells of *Ostrea edulis*, cuboidal or columnar in section, but of irregular shape if observed from above, are concerned in the deposition of conchyolin. In places where much conchyolin is required (e.g., in the formation of the ligament) these cells are very tall and important, while "mucus" glands are practically absent there (Korringa, 1951c). On the other hand, "mucus" glands are conspicuously large and numerous at the margin of the mantle, an important organ for shell deposition (Korringa, 1951b). Similar glands have also been found in other bivalves by Bevelander and Benzer. Intermediate conditions are

found in those parts of the mantle epithelium which are concerned with the thickening of the shell, both of the growth shoots newly formed by the margin of the mantle and of the older parts. This thickening is not mentioned by Bevelander and Benzer, who focused their attention on the mantle margin. According to these authors, calcium phosphate is probably formed first, but just how calcium phosphate is ultimately converted to the final calcified product, calcium carbonate, can only be conjectured at present.

The oyster finds the calcium it needs to construct its shell in great abundance in the sea water (about 1 gram per liter when expressed as $CaSO_4$). I rejected earlier (Korringa, 1951a) the view of Ranson (1939–1941) that the oyster collects the calcium it needs in inorganic particulate form. Even in places where small pieces of calcium carbonate will only rarely be caught by a feeding oyster, normal shell growth may occur. There is no correlation between shell deposition and the quantity of particulate calcium present on the bottom or in the water. Without doubt the oyster can extract the calcium ions which abound in all sea water in much the same way that it extracts and accumulates certain other metals (Fe, Cu, Zn, Fe, Hg, Mn). Proof that a bivalve does not get its calcium from either particulate calcium carbonate or from the food organisms it ingests is furnished by Bevelander and Benzer (1948), who found that repair of the shell is carried through even in artificial sea water devoid of food. Only if there was less than the 20 per cent of the calcium normally occurring in sea water was no shell secretion observed. In waters of normal salinity calcium is therefore never the limiting factor in shell growth, for the relation Ca:Cl is fairly constant in sea water all over the world. Humphrey (1941b) found that too, and the statement in the preface of his paper that "the rate of growth is undoubtedly influenced by the supply of calcium" is in contrast to his conclusion that "there is no essential difference in calcium content between waters where growth is normal and waters where only a stunted growth occurs." The calcium content is often lower in waters of seriously reduced salinity, but oysters may suffer from too low a salinity in many other ways, so that under such conditions poor shell growth is not necessarily caused by lack of calcium.

The oyster rarely secretes pure white calcium carbonate. Some pigment may be added, deposited by the mantle margin especially in the outer layer of the shell. The color of the exterior surface of the mantle margin clearly indicates where the pigment comes from. Oysters with dark-colored shells have a heavily pigmented zone in the mantle margin, while oysters with white shells have a pale mantle. Banded shells have a corresponding pigmentation of the mantle. It is not true that the pigmentation is of alien origin, as Poisson (1946) thought ("Les bords du manteau sont bourrés de parcelles figurés de argile colloidale et de matière végétale vert jaunâtre. C'est ce qui donne sur les bords de l'organe une petite bande colorée en brun, noir ou jaune.")

Shell growth occurs periodically. Like so many of the oyster's other activities water temperature is certainly a very important factor. This is not because deposition of calcium carbonate is impossible at lower temperatures, but because the oyster feeds actively only at higher temperatures, and it is only then that it feels the need of a larger and deeper shell. Growth is therefore limited to the warmer months, at least in temperate regions. Though continuous shell growth may occur in spat and yearlings in the summer season, shell growth may be interrupted in older oysters during the spawning period (Needler, 1941a; Ranson, 1949b). Some of the contradictory statements about this may be ascribed to the fact that usually only the shell's increase in diameter is measured, the period used for thickening the new shell shoot being considered as interruption of shell growth. However, accurate weighing might demonstrate that calcium deposition goes on as intensely as during the formation of shell shoots, which happens more or less rhythmically in individual oysters. There is, however, a second reason for conflicting statements on growth during summer. In waters rich in food spawning activities hardly lead to any interruption of growth. In waters which are constantly or temporarily rather poor in food, older oysters may show shorter or longer interruptions of shell growth during the season of reproduction. Though Ranson (1949b) mentioned such an interruption of growth of *Gryphaea angulata* on the parks of the Isle of Oléron, he has added that in the "claires" (fattening ponds) growth may be practically continuous. In the Oosterschelde I found a virtually non-interrupted growth in *Ostrea edulis* during summer (Korringa, 1951b). Careful weighing under water showed that as long as the water temperature remains above 10°C. the deposition of shell material goes on. Only above 15°C. was the diameter of the shells found to increase,

somewhat earlier in young oysters, somewhat later in the older oysters. In times of overpopulation of the Oosterschelde, interruption of growth did occur among the older oysters in the season of reproduction (Korringa, 1947a). This was probably caused by food scarcity, or by a generally poor condition of the oyster brought about by other causes. Unfortunately we have neither exact data on the food content of the water during these periods of overpopulation, nor a good method of measuring the food content of the water at this time. There are, however, many indications that only when sufficient food is available, will shell growth occur. Ranson (1949b), who stated that shell growth in *Gryphaea angulata* takes place between 10°C. and 25°C. when sufficient food is available ("à condition toutefois que l'alimentation soit suffisante"), records good growth in *Gryphaea angulata* on the coast of the Isle of Oléron in the wet summers 1921–1935 and poor growth in the dry summers 1935–1947. Though he was inclined to ascribe this difference to the direct influence of salinity, and even considered the local water table and the importance of submarine sources of fresh water, his observations on the excellent growth in the Portuguese oysters during the dry and hot summer of 1947, with high salinities prevailing, indicate that it is the food available to the oyster, rather than the salinity of the water, which determines whether or not growth will be sufficient. ("Il faut donc admettre en réalité que malgré la sécheresse et la forte salinité de l'eau sur la côte Oléronaise l'alimentation y a été substantielle en Juillet-Août 1947"). In many coastal districts food will be plentiful as a rule when rivers close by discharge much water, but other sources of nutrients (e.g., upwelling water) may sometimes be of equal importance.

It is interesting to find (Ranson) that oysters, the volume of whose tissues diminish in difficult times, still try to fill the entire shell cavity by thickening the shell ("Si le volume de ses tissues diminue, elle sécrète de la coquille en épaisseur et réduit l'espace intervalvaire"). This agrees with the observations of Medcof (1944a) and of Galtsoff, Chipman, Engle, and Calderwood (1947) discussed in the section "anatomy."

Here again it should be noted that abundance of food does not necessarily mean water rich in large plankton forms like diatoms and peridinians. It is not surprising that Baughman and Baker (1951) failed to find a correlation between the abundance of diatoms and the growth rate of oysters (*Gryphaea virginica*) in Texan waters. Gaarder and Alvsaker (1941) found excellent conditions for growth in water poor in diatoms, but rich in nannoplankton. Differences in feeding conditions among oysters living in the same body of water may lead to differences in growth. Thus Kerswill (1949) found a better growth in oysters (*Gryphaea virginica*) and clams (*Venus mercenaria*) when a better circulation of water was ensured in the containers in which they were kept. I could easily adduce similar evidence for oysters (*Ostrea edulis*) grown in trays in the Oosterschelde. Not only the number of oysters per tray, but also the way the trays are placed in the prevailing tidal currents greatly influences the growth of the oysters. Ranson (1949b) noted that the new growth shoots in *Gryphaea angulata* differ in breadth according to the position of the oysters, being less in those higher on the beds, and thus exposed for a longer time at low tide and consequently having shorter periods of feeding.

As stated above, shell growth usually parallels water temperature. Investigations carried through with *Gryphaea virginica* in the Milford laboratory, Connecticut (Loosanoff and Nomejko 1946a, 1949) demonstrated that no changes in shell diameter occur in the colder period December-March inclusive, when the oyster's activities are greatly reduced. Possible changes in shell thickness have not been measured in these experiments. Growth starts in April in the waters of Long Island Sound, is of great importance in summer, and decreases again later in the year. It is interesting that increase in length predominated in May, June, and July, that the breadth of the shell increased especially in May and June, and that the thickness of the oyster showed its main increase in July, August, and September. Computed as increase in total volume of the oyster, August and September appeared to be the months of most intense growth, and this is also the period of highest water temperature. Reproduction did not noticeably interfere with growth in the rich waters of Long Island Sound. In following growth in oysters (*Gryphaea virginica*) of different age classes, Loosanoff (1947), found that the volume of the oyster increases from 0.4 to 19.5 cc. in the first year. This he expressed as 4775 per cent, which compares favorably with 130 per cent in the second, and 44 per cent in the third year. Percentages are rather misleading here. If we begin the calculation at the time the spat settled, still more impressive percentages would be found. More important is the fact that the mean

dimensions reached by different groups of oysters upon attaining the same age corresponded rather closely in the area of investigation, e.g., 3-year-old, 70 grams; 4-year-old, 120 grams; 5-year-old, 150 grams. Perhaps greater differences from year to year would be found in other oyster districts, especially in those depending on rivers as a source of nutrients.

In Southern districts there may be no growth interruption in winter. Serbetis (1949) carried through a series of growth observations on oysters (*Ostrea edulis*) hung from racks at the Salamis experimental oyster farm (Greece). The graph he has presented seems to indicate continuous growth in these southern waters; at first the oysters grow rapidly, and later growth slows down. Upon a closer examination it appears, however, that the dates of measurement, though close together in the first few months, gradually became farther and farther apart, and the later intervals extended up to 6 months, so that the true course of growth may have been considerably more capricious than the graph actually suggests. Water temperatures are not given. Absence of winter stagnation in growth cannot be concluded from the data presented.

Gryphaea virginica may show very rapid growth indeed in Southern waters. Ingle (1950) has mentioned a diameter of 4.5 mm. at the age of one week, and of 8.0 mm. at two weeks, which finally led to 104 mm. after 31 weeks in the warm waters of Apalachicola Bay (Florida). Menzel (1951) stated that oysters may grow throughout the year in Louisiana waters and may attain a diameter of 50 mm. in 2 months, and 100 mm. within 9 months after setting. Similar data are recorded by Paul (1942) for *Gryphaea madrasensis*, which could attain 12 mm. in 21 days after setting.

Newcombe (1950a) studied the dimensional relationships of *Gryphaea virginica* from some natural beds. Oysters of different origin showed differences in ratios, especially in that of length to breadth but the product of length and breadth of the shells appeared to be remarkably constant and so were the non-linear indices of size.

XII. ECOLOGICAL RANGE

Data on the ecological range of adult oysters have been given in many a paper. Special attention has been paid to the extreme values of temperature and salinity which oysters can support. It has often been observed that many oysters may be killed by prolonged cold spells. Though oysters of the *Gryphaea* type require higher water temperatures for their reproduction than the flat oysters (*Ostrea*), the latter suffer more readily from low temperatures in winter. Severe winters often play havoc among the flat oysters (Orton, 1940; Ranson, 1943; Korringa, 1947a; Cole, 1951) even when they are never directly exposed to low air temperatures. Ranson mentioned −1°C. as lethal for *Ostrea edulis*. Such conclusions should, however, be drawn with care. The experience of Orton (1940) that Brittany oysters relaid in British waters suffer more readily than native oysters, tallies with our own observations in the Oosterschelde. Spärck too (1951) has noted that both French and Norwegian oysters are far more sensitive to prolonged cold spells than native Limfjord oysters are. British, Dutch, and Danish oysters can stand −1.5°C. (the freezing point of sea water of 27‰) for several weeks in succession. Dannevig (1946, 1951) noted that oysters brought from the Norwegian west coast to the Skagerak coast are more subject to mortality in winter than oysters raised in the ponds of Flødevigen on the S.E. coast of Norway. He is inclined to ascribe this phenomenon to differences in salinity, for he found that some winter mortalities in Norwegian waters earlier ascribed to low temperatures have indeed been caused by water of low salinity accumulating under the ice. I remarked earlier (Korringa, 1950) that it is often difficult to distinguish the effect of temperature from that of salinity in winter mortality. In the Oosterschelde, where low salinities do not occur, French and Norwegian oysters were found to be considerably more sensitive to prolonged cold spells than native Dutch oysters living under the very same conditions. Could it be that the high water temperatures prevailing in the Norwegian polls, and in the French centers of spat production exert their influence on the young oysters in such a way as to make them vulnerable in cold winters? Tank breeding experiments may give the answer in due course.

It is not known exactly how oysters are killed by low temperatures. Gaarder (1950) stated that death is brought about by the formation of ice crystals in the adductor muscle, but this can hardly hold good for oysters permanently bathed in water. Usually mortality sets in when the cold spell is over. Like Orton (1940), and Cole (1951) we have noticed that the dying oysters always contained much mud, especially on the gills. This mud is presumably accumulated during a gaping condition, due to relaxation and paralysis of the adductor muscle as a result of a prolonged period of low temperature. We have the impression that if rough

weather and turbid water prevail during the thaw, mortality is much heavier than in calm weather. Apparently the accumulation of mud on the gills and in the mantle chamber, of which the weak oysters cannot rid themselves, is an important factor in winter mortality. Perhaps the possibility should also be considered that prolonged low temperatures reduce the oyster's resistance to microbial infections, but there is as yet little scientific evidence to support that view.

Oysters of the *Gryphaea* type are hardier than flat oysters. According to Ranson, *Gryphaea angulata* can stand −5°C. for some time. This corresponds with the temperature below which the snail *Helix pomatia* freezes to death (Fischer, 1948). *Gryphaea virginica* may be killed in winter in shallow water (Needler, 1941a). In deeper water, according to Needler (1941b), the temperature may rise considerably after the formation of a complete ice-cover, so that there is little danger for oysters and many other invertebrates. It is said that *Gryphaea virginica* can even survive actual freezing under certain conditions and is then only killed if jarred or subjected to other rough handling. When thawed carefully with a minimum of handling it survives (Needler, 1941a; Loosanoff, 1946). Loosanoff tentatively ascribes the lethal effect of jarring to a rearrangement of ice crystals within the body cells of this mollusk, but it would be difficult to observe directly whether or not true ice crystals had already formed within the cells. Can it be that the cell contents were only undercooled and not really frozen, so that jarring suddenly gives rise to the formation of ice crystals which tear up the tissues?

The oyster's life may be endangered by high temperatures too. Loosanoff (1950a) found that *Gryphaea virginica* begins to show distress at temperatures above 34°C., resulting in a marked decrease in the rate of pumping and in abnormal shell movements. Ranson (1949b) noted that the growth of *Gryphaea angulata* ceases when a temperature of 30° to 32°C. is reached in the claires (fattening ponds). According to Fischer (1948) the functioning of the adductor muscle is weakened above 28° to 30°C. and mortality can be expected in oysters from 30° to 40°C. On the other hand, *Gryphaea rhizophorae*—which is perhaps only a variety of *G. virginica*—thrives throughout the year in the warm waters of some Puerto Rican lagoons in which the temperature often exceeds 30°C. (Mattox, 1949).

Many investigators have reported on the adverse effects upon oysters of too low or too high salinities, but several statements are contradictory. Everybody agrees that oysters of the *Ostrea* type are more readily damaged and killed by low salinities than oysters of the *Gryphaea* type. Though *Gryphaea angulata* can support short periods of very low salinity by closing its valves, it cannot stand a prolonged sojourn in too brackish water. Ranson (1943) noted damage below 13‰ (sp. gr., 1.010). The Portuguese oyster then develops oedemic tissues, with vacuolization of the epithelial cells and a sharp increase in the number of leucocytes. Below 7‰ (sp. gr., 1.005) the degeneration of the tissues progresses; the gills especially suffer. Similar observations have been made on *Gryphaea virginica*. Heavy mortalities have been observed on the upper bars of Chesapeake Bay (U. S. A.) in years when the Susquehanna River brought down exceptionally large volumes of fresh water. Thus the salinity was well below 10‰ for a prolonged period in the year 1945, and this affected the oysters adversely and ultimately led to a serious mortality for which no diseases or parasites could be held responsible (Engle, 1946). Butler (1949) carried through histological studies on oysters living under such unusually low salinities. He found that the oysters starved, since their filtering capacity is seriously impaired by low salinity. Possibly the food content too was lower in the brackish water, and perhaps the assimilation of the food collected was also unsatisfactory. The tissue starvation led to considerable delay in gonad differentiation and maturation, so that a spawning of limited magnitude occurred about seven weeks later than normal. Beaven (1946) demonstrated that many earlier mortalities on the upper bars of Chesapeake Bay can be correlated with a high run-off of the Susquehanna River, but not necessarily with extreme values of local precipitation. Six mortality periods in the years after 1900 correspond with the six highest sustained periods of cumulative run-off from the Susquehanna.

Careful experiments carried out by Loosanoff and Smith (1949) on the oyster's rate of pumping and shell movements showed that *Gryphaea virginica* can get accustomed to a much lower salinity than prevails in the water in which they were grown. In the laboratory oysters could be accustomed to salinities as low as 7‰ for a prolonged period. Such oysters stopped pumping when the salinity was lowered to 3‰, while oysters adapted to 27‰ stopped even at 12‰. Later experiments (Loosanoff, 1950b) showed that *Gryphaea vir-*

ginica is capable of withstanding sharp changes from low to high salinity without experiencing serious physiological injuries, and that it is tissue starvation due to a prolonged sojourn in water of very low salinity which may lead to the oyster's death. This corresponds with the information presented by Ingle and Dawson (1951), who found normal growth and survival of oysters in many stations in Apalachicola Bay, though the salinity there may vary from 0 to 42‰ in the course of the year. Salinities differing from week to week by as much as 11‰, and tidal changes in salinity of 4.8‰ did not interfere appreciably with the oyster's well-being. Medcof (1944b) has claimed, on the other hand, that *G. virginica* from Canadian waters is already affected and starves at salinities below 20‰. Apparently the critical value of the salinity is much lower on many oyster beds on the Atlantic coast of the U.S. It is not clear why. *Gryphaea* is usually considered as an estuarine invertebrate, because it thrives especially well under estuarine conditions (Ranson, 1943). This is no proof, however, that *Gryphaea* actually prefers waters of reduced salinity, since many other factors (e.g., the quantity of available food) differ from those prevailing in oceanic water. The slow growth of *G. angulata* in oceanic water (Ranson, 1940a) may very well be caused by factors other than salinity. Though Ranson (1940a, 1943) stated that *G. angulata* cannot thrive in water of a salinity above 31‰, this oyster grows and fattens exceptionally well in the rich and saline waters of the Etang de Thau on the Mediterranean coast of France. The same holds good for *G. rhizophorae*—very closely related to *G. virginica*—which thrives at salinities of 33 to 44‰ in Puerto Rico (Mattox, 1949). I am therefore inclined to support Fischer (1948), who stated that many so-called estuarine species have a wide ecological range and may endure the salinities of oceanic water very well. They thrive especially well in estuarine conditions because species which would compete with them in more saline water cannot endure the lower salinities in the estuaries. We can add that the abundance of food in many estuaries and the inability of many oyster enemies to live in brackish water facilitate the flourishing of oysters under estuarine conditions. No doubt many oyster beds (*G. virginica*) do exceptionally well in estuarine waters because drills, starfish, and the boring sponge cannot stand the reduced salinities prevailing there.

Oysters can stand exposure out of water for prolonged periods. This facilitates their transportation to no small extent. Oysters of the *Gryphaea* type are in this respect also hardier than flat oysters (*Ostrea*). Even tiny spat of *Ostrea gigas* can be transported by boat, packed in wooden boxes, for several weeks (Hopkins, 1946; Kincaid 1951). It is generally accepted that oysters live under anaerobic conditions when exposed to the air, as they keep their shells closed. It is not yet clear whether loss of moisture or respiratory difficulties sets limits to the length of the exposure period, and neither has it been investigated whether or not the oxygen of the air has any influence on oysters while out of water. A general statement like that of Fischer (1948), "Ce qui facilitait la tolérance respiratoire des mollusques c'est la robustesse de leurs tissues," explains little.

It has been noted in a previous section that a lowering of the pH value below 7.0 reduces the rate of pumping in *Gryphaea virginica* (Loosanoff and Tommers, 1947). This will not often occur under natural conditions.

Fischer (1948) rightly remarked that little is known on the physiological influence of sunlight on oysters and other mollusks. Medcof (1949) carried out some experiments in trays and found that oysters (*G. virginica*) exposed to sunlight formed a thicker, harder, and more deeply cupped shell than those growing in the dark, though the shells of the latter gained more in diameter. The oysters grown in the dark were leaner than those exposed to sunlight. Since, however, *Ulva* and other plant growths were abundant on and among the exposed oysters, and mussel seed and other invertebrates abounded among the oysters grown in the dark, it is difficult to deduce the degree to which the differences observed are directly due to sunlight. Indirect influence through differences in food production and competition were probably of considerable importance in Medcof's experiments.

In some cases it is important to know to what extent industrial pollution can endanger the well-being of oysters. The sulphite waste liquor of pulp mills especially has caused considerable damage. The lethal effect of high concentrations of sulphite waste liquor had been reported before, but the slow action of prolonged exposure to small concentrations of this dangerous pollutant is of no less importance. Odlaug (1949), who used several approved bioassay methods, found a reduced rate of pumping in *Ostrea lurida* at concentrations of 200 to 500 parts per million of sulphite waste liquor. At 1000 p.p.m. the oysters suffered greatly.

Such oysters develop a thin wa tery body and brow n shrunken gills. Such high concentrations are found only in the immediate vicinity of the pulp mills and not on the oyster beds. Evidence is adduced that at least some fractions of the pollutant undergo chemical and bacteriological breakdown when diluted with sea water, but there is no proof that the fractions toxic to oysters are readily disintegrated. Since Odlaug used the rate of pumping as the criterion, the possibility remains that more delicate processes in the oyster's physiology—such as the formation of mucous feeding sheets—are seriously impaired at concentrations much lower than those mentioned above.

McKernan, Tartar, and Tollefson (1949) demonstrated that a serious decline in the production of *Ostrea lurida* in Southern Puget Sound (Wash.) ran closely parallel to the activities of the Shelton pulp mill. Studies of tidal currents revealed that the pollutant of the pulp mill can reach the oyster beds within 24 hours. The investigators carried through a long-term experiment in wooden troughs. Even a concentration as low as 13 parts per million of sulphite waste liquor appeared to be harmful to the oyster. In higher concentrations the toxic effect appeared to be more rapid, with mortalities levelling off during the last five months of the experiment. A typical symptom caused by the pollutant is that the gill lamellae develop indentations along their edges. The investigators concluded that the lowest concentration dangerous for *Ostrea lurida* lies somewhere between 0 and 13 p.p.m. As the control oysters, kept in similar wooden troughs, also showed a rather poor growth and a considerable mortality, the experimental conditions were not ideal, and require improvement if one wants to find the lowest concentration of the pollutant which endangers the well-being of *Ostrea lurida*.

Similar results were obtained with *Gryphaea virginica*. Galtsoff, Chipman, Engle, and Calderwood (1947) made a study of the serious decline of the oyster industry in the York River. This decline appeared to run parallel to the activities of the pulp mill at Westpoint (Va.) The poorest oysters, emaciated, and with an unpleasant flavor, showing brownish or greenish discolorations of mantle, gill, and labial palps, were found in the upper part of York River, not far from Westpoint. Histological investigations revealed that such oysters often had abnormal fibers in the adductor muscle. Comparison of hydrographical and biological conditions in the York River with those prevailing in the nearby unpolluted Piankatank River revealed that factors like temperature, salinity, pH, O_2 content, predators and parasites, and phytoplankton production cannot be held responsible for the enormous difference in growth and fattening of oysters in those rivers. Using the pigment unit technique to measure the density of phytoplankton, it was found that the York River yielded even higher figures than the Piankatank. This agrees with the stimulating effect of low concentrations of pulp mill effluent on the growth of the diatom *Nitzschia* under laboratory conditions. The investigators realized, however, that their technique does not allow them to measure exactly the amount of living matter produced in the form of plankton, and also that decisive conclusions cannot be drawn before the nutritive value of the various forms comprising the phytoplankton has been ascertained. No data have been collected on the abundance of of the ultra-plankton, which may greatly contribute to the oyster's food. Transplantation experiments yielded very clear-cut results, and demonstrated that conditions impairing growth and fattening of oysters prevail in the upper York River. Glycogen content was lowest in the upper York River and highest in the upper Piankatank River. Intermediate figures were found for the downriver sections. Transplantation experiments also showed that the factors retarding growth and fattening in the upper York River inflict no permanent injury on the oysters. Laboratory experiments demonstrated that the pulp mill effluent reduced the oyster's rate of pumping. Clear-cut results were, however, only obtained with rather high concentrations of the pollutant (above 1‰), and a cumulative effect has not been found. These figures are considerably higher than those mentioned above for *Ostrea lurida*. Though flat oysters are in many respects undeniably more sensitive than oysters of the *Gryphaea* type, it seems probable that the threshold value below which no damage is inflicted is in reality much lower than the 1‰ mentioned by Galtsoff et al., for more delicate processes in the oyster's physiology may be affected at a lower concentration than the rate of pumping used in the bioassays. It is doubtful whether concentrations as high as 1‰ occur regularly on the affected oyster beds of the York River. Exact data are not available, since no adequate chemical reaction is known to measure the concentration of pulp mill pollutant and since some fractions at least of the pollutant are subject to chemical and biological breakdown in sea water. It has not been possible to determine

the exact chemical nature of the toxic fraction, but it seems probable that the highest concentrations occur in a sedimentation area several miles downstream from Westpoint.

We may also mention here Daugherty's paper (1950), in which it is noted that oysters show a decrease in irritability when 400 p.p.m. of sodium acid pyrophosphate—a compound used in some oil drilling operations—is added to sea water. Mortality occurred in concentrations of 500 p.p.m. (44 hours) and higher, but I presume that here too the threshold value below which no ill effects are caused in *Gryphaea virginica* may be much lower.

Two more papers should be mentioned in this ecological section. First is that by Caspers (1950), who studied the ecology of the biocoenosis of the declining Heligoland oyster bank. This bank appeared to belong to that part of the *Amphiura filiformis* community where the occurrence of *Nucula nucleus* is characteristic. The oyster bed is rich in species and individuals. *Tapes pullastra*, *Sabellaria*, and *Alcyonium* abound here. Fluctuations in the number of oysters exert their influence on this biocoenosis, not only with respect to animals closely associated with living oysters, but also more indirectly by changing the ecological conditions of the substratum, since shells and shell debris are liable to disappear in the long run.

In the second place there is my own paper (Korringa, 1951f) on the shell of living oysters as a habitat. The biocoenosis of the shell of oysters (*Ostrea edulis*) permanently bathed in water of a fairly constant salinity (Oosterschelde) appeared to be amazingly rich in species and individuals. Polychaete worms were especially abundant. Closer investigation demonstrated that most of the animal denizens of the oyster shell settle from the plankton, and further, that the oyster contributes little, if any, food for the inhabitants of its shell. It is the factor of shelter (against enemies and silting) which renders the shell of a living oyster so very attractive as a habitat. True parasites of the oyster have not been found on its shell. Among the many species found there, only *Cliona* and *Polydora* may endanger the oyster's well-being.

XIII. GONAD DEVELOPMENT

The primary sex phases and seasonal gonadal changes in *Ostrea edulis* have been studied by Cole (1942a). The age of his oysters—born in the Conway breeding tanks—being precisely known, and serial sections made, the data obtained are of great precision and reliability. Though both oogonia and spermatogonia appeared to be present in the tubular ducts of the young gonads, the prevalence of protandry appeared to be universal. Egg development begins well before sperm development has been completed. This, and also the fact that certain parts of the gonad often lag behind in development, led astray earlier investigators, who used the smear technique. True functional hermaphrodites probably do not exist at all in *Ostrea edulis*, but the transitional phases, containing both ripe sperms and developing eggs, are often found. Pure males without developing eggs are rare even early in the summer season, and so are ripe females without some sperm development. Only later in the season may a resting condition precede further sexual development. The rate of gonad development and sex change depends largely on temperature and food conditions. As a rule, British oysters do not function as males the same year they are born, but wait until their second summer. The largest individuals may then become functional females later in that same year. Older oysters will as a rule pass through both sex phases at least once a year in British waters. A high percentage hibernates in a transitional phase. The conditions prevailing in their second summer may determine for several years to come whether oysters of a certain year-class will be early summer spawners or late summer spawners.

Considerable information has been collected on gonad development in oysters of the *Gryphaea* type. Bargeton (1942), studying histological and chemical changes in the connective tissue of *Gryphaea angulata*, gave in the same paper a vivid description of the development of the follicles of the gonads in early summer, leading to the almost complete disappearance of its glycogen-bearing connective tissues.

Cleland (1947) has given detailed information, including photomicrographs, of the cytology of oogenesis in *Gryphaea commercialis*. He distinguished on the basis of cytological characteristics the following stages: a) the definite auxocyte, which is an oocyte just before it enters into the growth phase; b) auxocyte 1; c) auxocyte 2; d) auxocyte 3; and e) the mature oocyte, now free in the lumen of the follicles. Cleland noted that at all stages of oogenesis the chromosomes can usually be seen near the membrane of the germinal vesicle, as fine paired structures showing chiasmata. The diploid number—never recorded before in oysters—appeared to be 10, and the reduction division occurs after sperm entry. Many details are given on

the cytochemistry of the developing egg. Among other things the presence of phospholipids, a neutral fat, and a polysaccharide (probably glycogen) are recorded. The tyrosine content was found to increase during the development. The terms "mitochondria" and "Golgi-apparatus" are avoided by Cleland, and replaced by P-granula (yolk), absent in young oocytes, and L-granula, which do not change with the physiological state of the egg.

Loosanoff (1942) gave a clear description, illustrated with photomicrographs, of the gonadal changes in *Gryphaea virginica*. The sequence of events from the dormant winter stage, the growth of the follicles in spring, the rapid growth, ramification, and anastomosis of the gonadal follicles when the temperature of the water rises, together with the disappearance of connective tissues and their glycogen reserves, closely resembles those described by Bargeton for *Gryphaea angulata*. Not the slightest doubt remains that seasonal gonadal changes in *Gryphaea* differ greatly from those in *Ostrea*, with its frequent and rapid sex changes, as described by Cole. According to Loosanoff, sex change might occur in *Gryphaea virginica* late in October, after intensive proliferation of the connective tissues, when it is difficult to distinguish males from females. Slight gametogenetic activities with a slight expansion of the follicles may be observed at that time.

It appeared to be possible to induce gonad development in *Gryphaea virginica* in the winter season by simply raising the water temperature (Loosanoff, 1945c; Loosanoff and Davis, 1949). Even if little food is given, an apparently normal development of the oyster's gonads may proceed. At 15°C. ripe sperm can be found after 15 to 20 days, after 30 days some female oysters had fertilizable eggs, and spawning could be induced after 35 days. Spontaneous spawning occurred after 60 days at 15°C. More rapid was the development at 20°C. (ripe sperm in 10 days, fertilizable eggs in 15 days), and at 25°C. (ripe sperm in 5 days, spontaneous mass spawning the ninth day). Amazingly rapid was the development of oysters brought from the dormant winter stage into water of 30°C. Ripe sperm was found already on the third day, and after 5 days some females appeared to contain fertilizable eggs. Even oysters transferred in spring from low to high salinities responded to the increase of temperature in the laboratory and proceeded with apparently normal development of the gonads (Loosanoff, 1950b). It has been mentioned above that Butler (1949) found a considerable delay in maturation due to tissue starvation in oysters living under conditions of seriously depressed salinity.

In Southern districts oysters of the *Gryphaea* type may mature at a very early age. Menzel (1951) found features of both sexes in the very young and still immature specimens of *Gryphaea virginica*. In the warm waters of Terrebone Parish (La.) he found among 10 oysters under 28 days old 2 mature females and 4 mature males, the smallest mature female measuring only 9.0 x 7.5 mm. Counting the larval life at 12 days, a new generation could be expected in 40 days. With a local spawning season of 200 days this could lead to as many as 4 successive generations in one year! It is interesting to note that Menzel found indications which seem to confirm Burkenroad's earlier finding that a higher percentage of males can be found among young oysters attached to the shells of living older oysters than among those attached to empty shells.

Paul (1942), who placed collectors in Madras harbor at frequent intervals, said that he once found mature male and female individuals of *Gryphaea madrasensis* only 21 days old.

XIV. FECUNDITY

Interesting facts on the number of eggs in *Ostrea edulis* have been collected by Cole (1941). Flat oysters produce fewer eggs than oysters of the *Gryphaea* type, and also spawn all the eggs simultaneously, while *Gryphaea* spawns intermittently at intervals of several days. Cole found that the number of eggs produced increases considerably with the age of the oyster. British oysters one year old—those already functioning as females—produced on an average 91,600 eggs, 2-year-old oysters 218,100 eggs, 3-year-old oysters 462,000 eggs, and 4-year-old oysters as many as 902,900 eggs. It is true, Cerruti's (1941) figures for oysters of the same age are considerably higher, but this corresponds with the very rapid growth of oysters in waters as far South as Taranto (Italy). The number of eggs depends rather on the size than on the age of the oyster, at least in *Ostrea edulis*. Larger oysters certainly contribute considerably more larvae than do small, and thus are of greater importance for the rejuvenation of the stock. As a rule oysters spawning later in the summer season produce fewer eggs than those spawning earlier, presumably because much reserve food has already been used in the former in a preceding male phase. According to Cerruti (1941), oysters

spawning late in the season (September to December) produce only one-third to one-sixth the number of eggs produced by those spawning early in the season. Though factors like larval development and the difficulties met during setting are certainly of paramount importance, Cole (1951) agrees with me that the initial number of larvae produced is important and that good spatfalls of flat oysters can hardly be expected in seriously understocked fisheries, despite the known fecundity of breeding oysters. I have adduced ample evidence (Korringa, 1947b) that considerable fluctuations in the stock of breeding oysters exerted a noticeable influence on the number of larvae produced in the Oosterschelde, and thereby on the chances of spatfall. This tallies with the fact that in periods with a dense oyster population successful spatfall has occurred much more ferquently than in periods with a poor stock of oysters (Korringa, 1947a).

Whether relaid Brittany oysters contribute much to the natural spatfall is still a matter of dispute (Cole, 1941). I remarked earlier (Korringa, 1950) that absence of spat in places where considerable numbers of foreign oysters had been relaid (Spärck 1951) does not prove that such oysters did not produce viable larvae. In the Oosterschelde relaid Brittany oysters did produce on a large scale apparently normal and healthy batches of larvae, and we feel sure that they contributed considerably to the spatfall there in years when native Dutch oysters were scarce and in poor condition.

There are, however, without doubt factors other than the number of breeding oysters which determine the total number of eggs and larvae produced. Oysters of the *Gryphaea* type especially may show considerable differences in thickness of gonadal tissues, not only from year to year (Loosanoff and Nomejko, 1951), but also from place to place (Loosanoff and Engle, 1942c). In the latter case the gonad tissue was found to be about twice as thick in oysters on beds at a depth of 10 feet than in oysters living at 30 feet. Presumably differences in food conditions, which are most unfortunately difficult to measure, were involved.

Some controversy exists on the number of eggs produced by oysters of the *Gryphaea* type. Galtsoff claimed earlier that a specimen of *Gryphaea virginica* of normal dimensions produced 115,000,000 eggs in one single spawning, which may make 500,000,000 eggs in the four or five consecutive spawnings to be expected in this species. Burkenroad (1947) criticized Galtsoff's estimation and calculated that such a number of eggs, each egg measuring 50 μ in diameter, could never fit in a normal oyster's ovary. The possibility remains that considerable egg development takes place after each spawning, but that is not what Galtsoff meant. In his reply, Galtsoff (1947) calculated that the egg—being pear-shaped while in the ovary—is only 40 μ in diameter at the rounded portion and thus comes to a total volume for 500,000,000 eggs of 16 cc., which might possibly fit in a large oyster with a thick layer of gonadal tissue. That Galtsoff's estimation is really rather on the high side, even though he may not have misplaced a decimal point, as Burkenroad presumed, can be deduced from Cleland's information (1950b) that 1 cc. of closely packed eggs of *Gryphaea commercialis* (egg diameter, 50 μ) contains 15,000,000 eggs, which would indeed require an oyster of more than normal size for 500,000,000 eggs, if we balance the advantage of a pear-shape against the fact that no gonad is entirely composed of eggs.

Ranson's estimate (1940a) that *Gryphaea angulata* produces only from 1,000,000 to 2,000,000 eggs does compare rather poorly with Galtsoff's figure, but may be disputable too.

We may add that data like those given by Cole on the fecundity of oysters of different age classes are of greater interest than the number of eggs one large oyster could produce.

XV. SPAWNING

The old idea that spawning activities in the oyster run closely parallel to the actual water temperature is rarely supported nowadays. Statements like that of Navaz y Sanz (1942), "la emisión no se da con cierta abundancia más que a partir de los 18°, teniendo lugar las fuertes emesiones y abundante fijación del enjambre entre los 20° y los 22°," presumably are based rather on spatfall observations than on spawning data.

The phenomenon of sex-change in *Ostrea edulis* brings about a differentiation into early summer spawners and late summer spawners (Korringa, 1941a), though with a good deal of overlapping. Cole's (1942a) detailed histological observations confirmed this view.

Quantitative plankton samples, collected for many years in succession twice a day at comparable stages of the tidal cycle in the Basin of the Oosterschelde, made it possible to study the underlying pattern in the spawning of *Ostrea edulis* (Korringa, 1947b, c, d). Spawning usually starts here early in June but does not reach its height until late in June or early in July. It dies down

late in August. Some spawning takes place almost every day, but maxima of greater and lesser importance are observed every year. Those maxima appeared to be uninfluenced by the course of the actual water temperature, or by the water temperatures in the period preceding spawning. By pooling the data of many years the unavoidable irregularities due to imperfections of the sampling can be smoothed out. Thus a curve is found that clearly indicates that throughout the summer season spawning of *Ostrea edulis* in the Oosterschelde tends to attain maxima at both spring tides, which leads to the appearance of great numbers of larvae about 8 days later. The greatest peak in spawning occurs between June 18 and July 2. This makes it possible to predict the mass appearance of larvae long beforehand: between June 26 and July 10, about 10 days after full moon or new moon. It is difficult to understand in what way spawning and tides are correlated, but similar phenomena—and often of much greater precision than in *Ostrea edulis*—have been noted for other invertebrate animals. Rhythmic changes in water pressure have been tentatively suggested as possible factors in the oyster's lunar periodicity in spawning.

Sato (1948) recorded maxima in the spawning of *Gryphaea gigas* at spring tides at Matoya-wan (Mie Prefecture, Japan) but ascribed this phenomenon to the carrying of warmer offshore water to the shallow breeding grounds, which is supposed to accelerate spawning. This factor cannot be held responsible in the Oosterschelde, where the oysters are not subject to similar changes in water temperature.

Ranson (1940a) has claimed that the Portuguese oyster (*Gryphaea angulata*) cannot get rid of its eggs when salinities as high as 29‰ to 32‰ prevail. Such oysters suffer, may show a sudden mortality, and may even remain in poor condition for years, according to Ranson. In the brackish water of the Charente estuary (France) he found that about 95 per cent of the eggs produced were normal and viable, but in the parks of the Isle of Oléron, where high salinities prevail, only 5 per cent of the eggs produced were normal; the others were irregular and could not produce viable larvae. The excellent set of Portuguese oysters on the Oléron coast in the warm and dry summer of 1947 was explained by Ranson (1949b) in terms of transportation of brackish water, bearing larvae, from the Charente estuary towards the Oléron coast, and not in terms of ample spawning by the oysters of the Oléron parks, though the latter certainly were in perfect condition that year.

Bargeton (1943) has described the events after spawning in *Gryphaea angulata*. The anastomosed gonad follicles rapidly lose their mutual contacts, and then begin to retreat, closely followed by the intensely proliferating connective tissue. The remaining eggs and sperms are either ejected later or resorbed by phagocytes. Neither Ranson nor Bargeton stated whether or not the spawning of *Gryphaea angulata* shows a certain correlation with water temperature, and whether all the eggs are released simultaneously or intermittently as in *Gryphaea virginica*. The post-spawning events in the latter species resemble very closely those described for *Gryphaea angulata* by Bargeton (Loosanoff, 1942).

Nelson and Allison (1940), following up earlier investigations, made an attempt to analyse the physiology of spawning in *Gryphaea virginica*. They found that the mutual stimulation of both sexes is of a more complex nature than had hitherto been supposed. Not only is there involved the soluble hormone-like substance, described earlier by Galtsoff, but also an active principle associated with the protein of the sperm, and not occurring dissolved or suspended in fluid expressed from the oyster's testis. This principle, called diantlin by Nelson and Allison, appeared to exert its influence on oysters of both sexes and in all seasons. This is said to result in relaxation of the adductor muscle, enlargement of the gill ostia, and in increased speed of ciliary action. This all precedes the actual spawning, and presumably facilitates the passage of the eggs through the ostia. Nelson demonstrated later (1941) by studying the effect of certain drugs that a rapid increase in the rate of flow following administration of diantlin results primarily from separation of gill filaments within each plica through relaxation of the intraplical musculature. Nelson and Allison (1940) demonstrated that dead, fragmented, and frozen sperm still contain the active principle, and they succeeded in dividing it into a non-heat-coagulable basic protein and a nucleoprotein fraction, which together appeared to be as active as a freshly made sperm suspension. It was concluded that diantlin is either a protein itself or that a protein is an essential link in the chain of events which culminates in stimulation of the oyster.

The spawning of *Gryphaea virginica* in Long Island Sound, a district of great importance for the American oyster industry, has been studied

intensively. Loosanoff and Engle (1940) found that spawning starts early in July but that most of the oysters do not release all their spawn at once. In the deeper stations especially the majority of oysters retained considerably more sperm than in stations of moderate depth. Individual variations appeared to be so great that it is questionable whether the small samples taken (6 to 10 oysters at a time) are sufficient for drawing general conclusions regarding the regularity of spawning in Long Island Sound. It is interesting that there appeared to be a considerable lag between the time the water temperature reached 20°C.—often considered as the critical water temperature—and the time of spawning, though the oysters were morphologically and physiologically ripe then. This has been confirmed by later observations (Loosanoff and Engle 1942c). Spawning begins practically simultaneously at depths of 10, 20, and 30 feet, though slight differences in temperature and salinity occurred. It was again noted that oysters in shallow water were sooner spawned out than those living in deeper water. A certain percentage, though presumably ripe, postponed spawning for a considerable time. In such individuals spawning could not be induced in the laboratory.

That there is not in *Gryphaea virginica* a definite temperature level below which spawning is impossible has been demonstrated by Loosanoff and Davis (1950). Even at a temperature as low as 15°C. spontaneous spawning occurred after 90 days. The authors deemed it possible that the temperatures prevailing during the period of gonad maturation determine the temperature at which the first spawning will take place. Maturation may, however, proceed at temperatures too low for spawning. A different explanation was given by Stauber (1947, 1950), who pointed out the noteworthy fact that in areas as far apart as Prince Edward Island, Long Island Sound, and Delaware Bay the initiation of spawning is nearly simultaneous, though temperature conditions differ greatly. He deduced tentatively that there may be at least three physiological spawning varieties in *Gryphaea virginica*—coming into action at different temperature levels—which might be the result of a long period of geographical isolation. Ingle's finding (1951) that the critical temperature for mass spawning is higher than 25°C. for the oysters in Apalachicola Bay seems to support Stauber's view, but Ingle has rightly remarked that "the existence of physiological races cannot, in any case, be demonstrated until the characteristics have been shown to be inherited"; further, that "distinct care should be taken not to ascribe spawning reactions entirely to temperature," for "conditions which determine the time of ripening of the gonad may be of greater importance than the stimulus which initiates spawning." Laboratory experiments on gonad maturation and spawning under controlled temperature conditions, like those carried out by Loosanoff, might demonstrate how far Stauber's assumptions are correct.

Having learned about the lunar periodicity in spawning in *Ostrea edulis* in the Oosterschelde, Loosanoff and Nomejko (1951) scrutinized their data in order to find out whether or not a similar phenomenon could be found in *Gryphaea virginica* in Long Island Sound. As this oyster shows a rather slow and gradual discharge of spawn, often with intervals of several days, very clear-cut maxima in spawning could hardly be expected. The distribution of larvae being very irregular and often even mysterious in Long Island Sound, plankton samples there appeared to be too poor a measure for the intensity of spawning. Data are available, however, on the initiation of spawning and on the intensity of setting. Spawning begins here between June 26 and July 3, probably independent of lunar phases, but reaches its height some time later. Setting shows two distinct peaks as a rule, the first one some 13 to 24 days after the beginning of spawning, the second 23 to 53 days later, but very often about 36 days later. The first setting peak does often occur at about the first quarter, but the second peak comes more than one lunar month later. It is difficult to use maxima in setting to study maxima in spawning, as the duration of pelagic life is not precisely known but presumably varies from 13 to 24 days. Taking as an average 18½ days, this would bring the spawning maximum of the first setting peak at the full moon spring tide, but that of the second setting wave at about the first quarter. Such conclusions should, however, be drawn with the greatest care. Not only because full moon and new moon spring tides differ greatly and often inversely in amplitude in Long Island Sound (this in contrast with the Oosterschelde), but also because it would certainly be impossible to obtain a clear-cut picture of periodicity in spawning in the Oosterschelde from the data on the intensity in setting. Too many factors influencing larval life and setting conditions interfere and obscure the picture. Loosanoff and Nomejko concluded that the data collected

thus far do not throw much light on the pattern of spawning in Long Island Sound. No explanation could be offered for the noteworthy fact that as a rule two marked setting peaks occur here, while setting usually dies down to zero in the intervening period. Can it be that two physiological races, in the sense of Stauber, live in Long Island Sound, one spawning early in the summer, the other much later? Or should we presume that the oyster usually shows a second spawning period here after an intervening period of rest? It seems improbable that it is a rapid sex change which brings about a differentiation into early summer spawners and late summer spawners as in the flat oyster, *Ostrea edulis*.

Finally we may mention some recent information on spawning in *Gryphaea madrasensis* in the harbor of Madras. Paul (1942) noted a maximum in the spawning season from April to May, decreasing slowly until October, but even in the non-reproductive period from November till March well developed gonads may be found and some spat will settle on artificial collectors in any month. Anon. (1950b) carried through histological investigations and found large-scale spawning in March and April, recovery from June to September, well developed gonads in October, and a second wave of spawning in November and December. Some larvae of this oyster may, however, be found throughout the year in the harbor of Madras.

XVI. FERTILIZATION

In a discussion on the conditions prevailing on very poorly populated natural beds of *Ostrea edulis*, I questioned whether sperm could be so scarce in the water that incomplete fertilization would occur (Korringa 1946a, b). This would be a great drawback for the rehabilitation of such beds. On the well-stocked beds in Holland I never found unfertilized eggs on the gills of incubating oysters. Cole's histological investigations (1942a) revealed that in ripe females there may or may not be a few ripe sperm balls remaining in the ducts of the gonad. From this, Orton (1946) concluded that self-fertilization will often be possible in *Ostrea edulis*. He added that it is not known whether cross-fertilization occurs, though this is biologically probable. This certainly is an interesting problem worth further investigation, especially in connection with studies on heredity and selection in oysters. Both laboratory experiments with individual oysters, and observations on very poorly stocked natural beds in the season of reproduction could tell us whether self-fertilization, cross-fertilization, or both, occur in *Ostrea edulis*.

XVII. EMBRYOLOGY

The osmotic properties of the unfertilized egg of *Gryphaea virginica* have been studied by Lucké and Ricca (1941). The rapid swelling and shrinking of the eggs in hypotonic and hypertonic solutions was measured quickly and intermittently by a special diffraction method. The authors consider the egg of *Gryphaea virginica* as an almost ideal osmometer, since swelling and shrinking are completed within 5 minutes and are moreover for a wide range of salinities completely reversible. Eggs swollen in sea water of a salinity of about 12‰ maintained the new equilibrium for many hours and regained their original diameter in normal sea water. This makes it unlikely that swelling in the hypotonic solution led to injury and consequently to loss of semipermeability. In this connection it is good to remember that Clark (1935) found earlier that the developing egg and young larva of *Gryphaea virginica* have a wide ecological range so far as temperature and salinity go. Not only could both sperms and eggs stand temperatures as high as 37° to 40°C. for some time, but the swimming stage was reached at temperatures from 15° to 30°C. and in salinities from 14½‰ to 39‰. The sperm appeared to remain active in salinities from 4½‰ to at least 41‰.

Lucké and Ricca also worked with diethylglycol, glycerol, and similar products, and found that the oyster egg, because of its high degree of permeability, could be considered as a natural osmometer particularly suitable for the study of the less readily penetrating solutes.

Cleland (1947) studied the osmotic properties of the egg of *Gryphaea commercialis*. Osmotic pressures ranging from 50 to 180 per cent of original sea water (15‰ to 54‰ salinity) were considered as harmless, since they did not lead to changes in granula integrity. The eggs are apparently naturally resistant to such changes in osmotic pressure. At pH values between 5.0 and 9.5 no internal changes could be observed within an hour.

Later Cleland undertook a study of the metabolic changes during the development of the egg of *Gryphaea commercialis*. He first studied the metabolism of the unfertilized egg (Cleland, 1950b). Detailed biochemical information is given on the contents of the egg. Among other products a considerable amount of free amino acids was detected, but this was not metabolically active.

From 90 to 95 per cent of the respiration of the egg appeared to be mediated by the cytochrome/cytochrome-oxidase system. The presence of malic oxidase and of succinoxidase could also be demonstrated. Experiments with inhibitors demonstrated that phosphate-bound energy is generated during respiration.

Next, the respiration of the fertilized and developing oyster egg was studied (Cleland, 1950a). Unfertilized eggs kept for 7 hours in Warburg vessels did not alter their rate of respiration. Fertilized and developing eggs showed a rapid increase in respiration during the first cleavage, next levelling off, and later rising again. The more synchronous the development of the eggs, the more pronounced was the observed rhythm in respiration. Apart from the study of the natural rhythm in respiration, correlated with phases of special activity in the embryo, experiments were carried out on the influence of pH (under pH 5.9, oxygen consumption appeared to be considerably lower than normal) and of colchicine, which abolishes the rises in respiration rate during development. Colchicine gives only a slight depression in the respiration of the unfertilized egg. Cleland's findings are interpreted in terms of activity and maintenance fractions of the total respiratory metabolism. The respiratory quotient was found to be 0.80, which is, according to Cleland, apparently due to combustion of a mixture of carbohydrates and lipids.

Nelson (1946a) made some interesting observations on the movements of embryos of *Ostrea cristata* (syn. *O. equestris*) during incubation in the oyster's branchial chamber. The movements of the embryos in the late blastula stage were not haphazard, but followed a certain pattern, which Nelson described. It was remarkable that the blastulae evoked no mucous secretion from the gills, though the eggs of *Gryphaea virginica* were quickly entangled.

Morphological features of the larvae of oysters and other lamellibranchs were given by Sullivan (1948) and by Rees (1950). The former has given both general characteristics and distinctive features and limited herself to the bivalves occurring in Malpeque Bay (P.E.I., Canada). The latter has built up a more general system for the identification and classification of lamellibranch larvae, and made special use of the hinge structure of the larval shell. Both papers are illustrated with many photomicrographs.

XVIII. PELAGIC LIFE

To obtain information on the duration of the pelagic period under natural conditions, one can try to follow the growth and development of the oyster larvae in the plankton. Especially in years with marked peaks in spawning it is not too difficult to follow a given brood of larvae. By means of this technique Needler (1940a) concluded that the larvae of *Gryphaea virginica* have in Canadian waters a pelagic life of 30 days at 18°C., of 26 days at 20°C., and of 24 days at 21°C. This is a longer swimming period than is usually recorded for U. S. waters, where the larvae also settle at a smaller size than in Canadian waters. It was found for *Ostrea edulis* (Korringa, 1941a) that after release the larvae have a pelagic life of 6 to 7 days at 22°C., of about 10 days at 20°C., and of about 12 days at 18°C. We may expect that these data, which are not very precise, will be corrected in due course as the technique for growing larvae under controlled laboratory conditions advances. Davis (1949) reared the larvae of *Ostrea lurida* till setting in 10 to 23 days at temperatures of about 20°C. A pelagic life of about 16 days was considered as normal in his experiments. This is a considerably shorter pelagic period than is generally found under natural conditions in Puget Sound. We wonder what factors can be held responsible for this discrepancy. At temperatures below 18°C. Davis' larvae did not metamorphose at all, even after a pelagic life of 30 days' duration. Under 16°C. the larvae lived for about 20 days, but did not grow to a size over 220 μ. Serious retardation of growth and development due to low water temperatures is a widely recognized phenomenon of great practical importance. That the early development of the egg also is greatly slowed down by low temperatures had been shown earlier by Clark (1935) for *Gryphaea virginica*.

There are conflicting views on the influence of the salinity on the development of oyster larvae. Though Clark's experiments and also the work of Lucké and Ricca, and of Cleland, (all mentioned in the previous section), indicate that eggs and young larvae of oysters of the *Gryphaea* type have, so far as salinity goes, a very wide ecological range indeed, Ranson is of quite a different opinion. He has stressed repeatedly (1941b, 1943, 1948a, 1949b) that oyster larvae cannot develop normally in waters of the salinity prevailing in the open sea. According to him oysters of the *Gryphaea* type require salinities even under 23‰ for the

development of the larvae. He claims that it is especially the factors of temperature and salinity which determine whether or not larval development will be normal, other factors being of minor importance. "Chaque espèce d'huître réclame une salinité et une température spéciale. Le développement de l'oeuf et de la larve a lieu entre des limites assez étroites en égard à ces deux facteurs. L'adulte en admet de plus larges" (Ranson, 1948a). With this hypothesis, applied rather dogmatically, Ranson has tried to explain many peculiarities in the setting of oysters. Thus the fact that the larvae of *Gryphaea angulata* only rarely develop normally in the waters around the Isle of Oléron is said to be due to too high salinities in these waters. Except in dry years, the more brackish waters of the Charente estuary may, however, be transported to the east coast of the Isle of Oléron (Saint-Trojan), carrying along developing larvae of *Gryphaea angulata*, which may thus lead locally to a set of commercial importance. Only larvae arriving in advanced stages of development will survive and settle on the coast of Oléron island. According to Ranson, it was the composition of the plankton which indicated the estuarine origin of the water (Ranson, 1941b). The year 1947 was both warm and dry, but in spite of this the setting of Portuguese oysters was abundant in the Oléron waters. Though the Charente river probably had a very moderate outflow that summer, Ranson claimed that very special oceanographical conditions must have carried that water with its Portuguese oyster larvae towards the Oléron coast: "a permis au courents de jusant de refouler sur les côtes Oléronaises une très grande quantité d'eau saumâtre de l'embouchure des rivières, contenant de nombreuses larves d'huîtres portugaises" (Ranson, 1949b). It is not explained where the presumably large volumes of water came from in that dry summer, and no data on salinities in the Oléron waters, demonstrating the influx of brackish water, have been presented in Ranson's paper. Ranson even claimed that the many young Portuguese oysters collected with tiles in the Basin of Arcachon (France) have no relation whatever to the many Portuguese oysters grown in that water, because the salinities prevailing there prohibit normal larval development of *Gryphaea angulata*. He supposes that larvae born in the Gironde estuary are carried along the coast in rather brackish pockets of water and next are swept into the Arcachon Basin: "Par ailleurs, les courents de jusant refoulent sur la côte landaise et particulièrement dans le Bassin d'Arcachon quelques éléments des eaux de la Gironde et y entrainent des larves d'huîtres portugaises que se fixent sur les collecteurs. Ce ne sont certainement pas les huîtres déposées dans le Bassin qui ont donné les larves en question, les conditions requises pour la reproduction n'y étant pas réalisées" (Ranson, 1949b). No data on currents, salinities, or larvae of different developmental stages are given to support this view.

It would be very interesting to learn on what grounds Ranson erected this daring hypothetical structure. It certainly cannot be his observation that the egg of *Gryphaea angulata* shrinks in water of a salinity of 31‰, swells a little in water of 23‰, and very much in water of 12‰, to which he adds rather mysteriously: "L'équilibrium intracytoplasmique de cet oeuf est tel que l'imbibition de la phase hydrophile commence seulement lorsque la salinité du milieu extérieur est relativement basse. C'est pourquoi le développement de l'oeuf de cette espèce n'a lieu que dans des eaux de densité 1010-1018" (Ranson, 1948a). For we have seen in previous sections that eggs of oysters of the *Gryphaea* type not only can stand a wide range of salinities without injury, but can even develop apparently normally in waters of greatly differing salinity. Nor can it be Ranson's observation that oyster larvae fail to develop in waters where a high salinity prevails (e.g., the coast of Oléron), for we have no proof that factors other than salinity are optimal there for larval development. Until Ranson gives a detailed description of the experimental evidence on which he has based his conviction, we feel very reluctant to accept his view that oyster larvae have a narrow ecological range so far as salinity is concerned, and that oysters of the *Gryphaea* type require salinities under 23‰ for normal development. Not only do the experimental data discussed above point in quite a different direction, but so do the many observations on excellent reproduction of *Gryphaea* oysters at high salinities: *Gryphaea madrasensis* reproduces all the year round in the harbor of Madras, where salinities vary from 30 to 34½‰ (Paul, 1942); *Gryphaea rhizophorae* settles all year round and often in great numbers in a lagoon off Boqueron Bay (Puerto Rico), where salinities vary from 35 to 40‰ (Mattox, 1948, 1949). Only in a rather shallow inlet where salinities of 44‰ prevail was setting poor and irregular. *Gryphaea gigas* settles year after year on a commercial scale in Magoku-Ura inlet (Myagi Prefecture, Japan), where salin-

ities vary between 30‰ and 32‰ in summer (Imai, Hatanaka, Sato, and Sakai, 1951). We feel sure that Ranson will presume that some influx of fresh water from brooklets or submarine sources must have given these larvae a chance to develop in brackish pockets of water, but the presence of such pockets has not been demonstrated though the authors mentioned studied hydrographical conditions in detail. Ranson (1948a) rejected the experimental data obtained earlier by Amemiya (1926), who found that eggs of *Gryphaea angulata* develop at salinities from 21‰ to 43‰, with an optimal range of 28‰ to 35‰, and eggs of *G. virginica* between 15‰ and 35‰, with an optimum of 25‰ to 29‰. Ranson did not carry through rearing experiments himself, but even if he had not been able to reproduce Amemiya's experimental data, we should consider the possibility that the salinities prevailing in the waters from which Amemiya's oysters came might exert an influence on the salinity toleration of the larvae. Perhaps physiological races in Stauber's sense exist in regard to salinity, too. Further, anybody who has seen the wide range of salinity in which *Gryphaea virginica* reproduces along the Atlantic and Gulf Coast of the U. S. (e.g., in Long Island Sound at 27–28‰) will be very hard to convince of the correctness of Ranson's view.

In his 1948a paper Ranson gave as the salinity range for the normal development of *Ostrea edulis* 25–28‰, of *Ostrea lurida* 18–23‰ (though salinities of 27–28‰ prevail in the oyster districts of Puget Sound; Hopkins, 1937), of *Gryphaea angulata* 18–23‰, of *Gryphaea gigas* 18-23‰, and of *Gryphaea virginica* 12–19‰. No experiments were described to support these figures.

Assuming that *Gryphaea* larvae require low salinities and high temperatures for development, Ranson (1951c) advanced the hypothesis that the spat of *Gryphaea margaritacea* found on collectors placed in Knysna Bay (Cape Province, S. Afr.), and also the adult oysters of this species attached to rocks along the South African coast, come from parents living as far away as Tuléar on Madagascar, where natural beds of this species occur. On this view not only must the larvae produced there be swept along with the sea currents from the first few days of their existence, but they must also develop in rather brackish pockets of water in these ocean currents, and cover some 2000 to 3000 km. before they reach Knysna Bay, and all this within 3 weeks, although the average speed of the Agulhas current is well under 50 miles per day. I should certainly be amazed if this hypothetical view were found to hold good. Not only because much richer beds of *Gryphaea margaritacea* (from which oysters are taken commercially on a fairly large scale) exist along the South African coast than Ranson has assumed ("on ne trouve que des échantillons dispersés"), but also because there is as yet no experimental evidence that *Gryphaea margaritacea* and other species of this genus have such a narrow ecological range as Ranson claims. Laboratory experiments with the rearing of larvae under well-controlled conditions should in due course throw more light on this problem. Such experiments offer no serious difficulties so far as the early developmental stages go, before the food factor comes into the picture.

There is a very important factor in larval development which Ransom has hardly mentioned, but which might very well be found responsible for many failures in larval growth in waters of high salinity, viz., the food factor.

That so very many efforts to rear oyster larvae in the laboratory have met with failure, though temperature and salinity left nothing to be desired, is generally ascribed to food deficiencies. Bruce, Knight, and Parke (1940) were virtually the first to develop a good laboratory method for rearing oyster larvae. They kept the larvae in plunger jars placed in subdued light, used offshore water, and fed the larvae with cultures of several types of naked flagellates measuring from 3 to 6 μ. Although in two experiments 90 and 99 per cent respectively of the larvae were reared till setting, we agree with Gross, who reviewed their work (Journal du Conseil, XV, 1947, p. 86) that the inconsistency of the results obtained with one and the same organism in successive experiments throws some doubt on the assessment of the food value of the different flagellates used. The suitability of naked flagellates as food for oyster larvae is now generally accepted by European workers. Dannevig et al. (1945) described successful rearing of oyster larvae in the laboratory on a diet of flagellates, but failure if non-motile algae of the chlorella-type were used, though these were readily ingested by the larvae. Cole's (1938) system of breeding oysters in tanks is based on creating suitable food conditions for the larvae by raising the number of small naked flagellates, to which end the water is enriched with minced crabs. This repeatedly led to success in the Conway purification tanks, and also in other deep tanks (Hughes, 1940; Wilson, 1941). Similar experiments have been carried out

in a deep tank at Flødevigen, Norway (Dannevig et al., 1945). Though success often alternated with failure there, the many observations carried out during these efforts clearly demonstrate that it is not the factors temperature, salinity, pH, or oxygen content which can be held responsible for the varying results, but that it is almost certain that the food differed greatly and was often unsuitable for oyster larvae: "Planktonundersøkelser bekrefter at resultat av yngelproduksjonen i bassenget i første rekke avhenger av næringsforholdene det vil si av planktonets utvikling." The years with an abundant nannoplankton (e.g., 1938) were especially successful. That it is not the quantity so much as the quality of the plankton produced which is decisive is clear from poor results in years when unsuitable plankton organisms—such as *Prorocentrum micans*, which is too large a food for oyster larvae—were abundant (1943). The presence in the basin of great numbers of older oysters was also found to lead to unfavorable food conditions (1939). Since it was not possible to control the quality of the plankton developing in the basin, it has not been feasible to stabilize the output.

Appreciation of the importance of very small nannoplankton organisms as food for marine larvae is growing. Cole and Knight Jones (1949b) described new methods of studying quantitatively the distribution and seasonal variation of these minute creatures. It is, however, still very difficult to distinguish small non-motile algae of 1 to 2 μ diameter from bacteria and minute particles of detritus. Cole and Knight Jones counted from 5 to 70 nannoplankton organisms per mm^3 of coastal sea water and up to 200 per mm^3 in the Conway rearing tanks. In the Oosterschelde I found from 1 to 8 small flagellates per mm^3 during the summer months (Korringa, 1949a).

A tank breeding method for oyster larvae based on the use of naked non-colored flagellates as food has been developed by Imai and Hatanaka (1949, 1950). These flagellates feed in their turn on bacteria, developing on naturally present or artificially added organic matter. Though the absence of light prevented growth of diatoms and other pigmented organisms, it appeared to be difficult to control the quality and quantity of food organisms. In too dense cultures of the non-colored flagellate *Monas* the oyster larvae failed to develop. The density of the oyster larvae was limited in Imai's experiments, and no irrefutable proof was given that it is really the *Monas*, and not bacteria or other kinds of food, on which his oyster larvae developed. Imai and Hatanaka (1950) observed small particles, presumably bacterial cells, rotating inside the stomach of the oyster larvae, but the flagellate *Monas* appeared to collapse soon after being ingested. From this Imai and Hatanaka concluded tentatively that the transformation of bacteria into *Monas* cells render them more readily digestible for oyster larvae, even if it does not increase the real food value. However interesting this observation may be, it is not yet convincing, since we are too poorly informed about the digestive process in oyster larvae. The possibility should be considered that bacteria are an easier object for intracellular digestion than burst *Monas* cells.

From 22 to 74 per cent of the larvae introduced by Imai and Hatanaka are said to have been reared to the setting stage. An interesting development is the biological control of the larvae of the mosquito *Aedes togoi* (which feeds on oyster larvae) with the aid of a fish big enough to enable oyster larvae to escape through the gill rakers.

That non-colored flagellates like *Monas* may constitute a suitable food for oyster larvae under natural conditions, too, is indicated by the observations of Imai et al. (1951) that successful larval growth and setting of *Gryphaea gigas* in Mangoku-Ura inlet (Miyagi Prefecture, Japan) coincided repeatedly with the occurrence of large numbers of such flagellates in periods when eel-grass leaves decay on a large scale. Bacteria too abound in these periods, but according to Imai and his collaborators these serve only indirectly as food for oyster larvae, since they are eaten by *Monas* and similar non-colored flagellates.

Tank breeding experiments, however interesting from a practical point of view, will never give the exact answer to what really constitutes the best food for oyster larvae. Only laboratory experiments under carefully controlled conditions, and the use of really pure cultures of microorganisms as food, can yield clear-cut results. Even then great care is required, for elements in the culture medium used for growing the microorganisms may exert an influence, as Gross rightly notes in his review. It therefore seems advisable to wash the food organisms thoroughly with the apparatus described by Cole and Knight Jones (1949b) to free them from bacteria and dissolved products.

Davis (1950a) has found that the larvae of *Gryphaea virginica* are especially difficult to rear in the laboratory, even when several types of microorganisms are used. He obtained some posi-

tive results with a *Chlorella* culture, but as no consistently good results have been obtained with this food, it seems probable that at least in the early developmental stages some contamination in the *Chlorella* culture constituted the crucial food. The results obtained thus far do justify Loosanoff's conclusion (1950c) that the larvae of *Gryphaea virginica* are probably quite selective in their food and may often perish before reaching metamorphosis because of the absence of the proper quality and quantity of food in the plankton. Needler (1941a) too has supposed that many larvae fail to obtain sufficient food, and also Blanco, Villaluz and Montalban (1951) have assumed that the presence of adequate amounts of suitable nannoplankton organisms is a crucial factor in larval development.

We are inclined to deduce both from results of rearing experiments and from observations under natural conditions that the larvae of *Gryphaea* oysters are more difficult and exacting in their feeding than are the larvae of *Ostrea*. Can it be that this is the reason why prolific natural beds of *Gryphaea* oysters are usually found in rich estuarine waters?

There are, however, experimental observations which indicate that even if small naked flagellates of the right type are abundant, and the physical factors leave nothing to be desired, oyster larvae often fail to develop. Tank breeding is not yet a foolproof procedure and one often fails, especially in shallow tanks. I have myself experienced how precarious tank breeding is in shallow water (Korringa, 1951e), and have collected evidence which led me to advance the hypothesis that metabolic excreta, products of vigorous assimilation or dissimilation, may not only stop larval development but may eventually lead to the untimely death of the oyster larvae. Foerster (1947) came to the same tentative conclusion, and perhaps one of the secrets of Imai's success is that he filtered all the water used through charcoal, which adsorbs much organic matter, and kept further production of toxic metabolites down by screening off the sunlight and by being very careful in enriching the water (½ g. starch per m^3 if necessary).

I feel sure that the possibility that both natural inshore waters and the water of rearing tanks and laboratory jars may sometimes contain toxic products deserves careful experimentation. Until we know more about it, it will be difficult to distinguish the possible influence of toxic metabolites from the complaints about lack of vitality of the oyster larvae. Though it is probable that Cole (1941) was right in stating that broods showing a great variation in size among the individual larvae show a poor survival under experimental conditions, and that the remark of Dannevig et al (1945) ("Det er erfaringssak at seint gytte larver har mindre chanser for å vokse opp en de som er gytt tidlig på sommeren") holds good, we agree with Bruce, Knight, and Parke that certain responses are as yet obscure and still demand further investigation before a consistent production under tank and laboratory conditions can be expected.

Of practical importance are data on the losses oyster larvae suffer under natural conditions. I adduced evidence myself (Korringa, 1941a) that the action of tidal currents causes only about 4 per cent of the water—carrying along with it its oyster larvae—to disappear from the Basin of the Oosterschelde in each tidal cycle. In many estuaries hydrographical conditions will not ensure such a high degree of retention of the larvae. In the Oosterschelde the losses suffered through other causes, probably especially through the activities of plankton-eating animals, predominate. About 10 per cent of the larvae produced here reach the setting stage at 22°C., when the pelagic life lasts approximately thirteen tidal cycles, about 5 per cent at 20°C. (19 tidal cycles), and about 2½ per cent at 18°C. (23 tidal cycles). The total losses per tidal cycle are calculated at about 14 per cent on an average.

Cerruti's observations and experiments (1941) are very interesting. Investigating why larval development and setting of *Ostrea edulis* failed in recent years in the Mar Piccolo near Taranto though many adult oysters produce their larvae there, and though setting was abundant some fifty years ago, Cerruti described several factors which may be injurious to oyster larvae. The water of the Mar Piccolo has been seriously polluted and was formerly "incomparabilmento piú puro di quelle d'oggi." In warm summers the muddy bottom may smell of hydrogen sulfide and the oxygen may be reduced, though it is rarely completely absent, in the deepest water layers. Cerruti has made interesting observations on the fate of oyster larvae caught by a variety of plankton-eating animals. Oysters, mussels, and many other lamellibranchs ingest the oyster larvae, but cannot digest them. They are still alive when ejected with the feces, but cannot free themselves from this sticky matter, and so perish. *Polydora* and *Balanus* may feed on oyster larvae too, but are able to di-

gest them, and so are many young fishes, the jellyfish *Aurelia* and its ephyrae, and the chaetognath *Sagitta*, which definitely hunts for oyster larvae. *Ciona* and other ascidians also ingest many oyster larvae, but are just as wasteful in their feeding as oysters and mussels, the larvae being still alive in the feces, but unable to free themselves.

Though Cerruti's observations are very interesting indeed, he has not demonstrated why larval development fails nowadays in the Mar Piccolo. He has claimed that larvae may be caught and killed in layers of water with even a trace of hydrogen sulfide, as they will not swim in such water, but such water layers rarely occur in the Mar Piccolo. If we compare, moreover, the conditions in the Norwegian oyster polls, where larval development is excellent though the deeper water layers are rich in hydrogen sulfide, we feel that this cannot be the main reason for failure in the Mar Piccolo. Cerruti stated further that mussel farming has increased greatly in importance in the Mar Piccolo, and although we know that both the mussels and their epibionts (ascidians, barnacles) destroy incredible numbers of oyster larvae, we can hardly believe that this leads to such tremendous losses that experimental collectors fail to collect any young oysters nowadays. Perhaps the increased pollution of the water holds the key to the problem. Can it be that too rich a nannoplankton renders the water toxic for the delicate oyster larvae? Observations in this water in August, 1938 on a case of red tide—which is only an extreme case of poisonous conditions brought about by the plankton—point in this direction.

We feel that oyster larvae generally can do very little to escape from the many dangers threatening them. They are defenceless against the tidal currents and against the plankton-eating animals. We can therefore hardly believe in a positive influence of a "survival of the fittest," such as Fischer (1948) has advanced: "Les individus que surmontent l'épreuve de la vie embryonaire prouvent par avance la robustesse de leur organisme."

Since many larvae may be swept away by the currents to places where setting is impossible, it is of great interest to find out how they behave during their pelagic life, and whether or not vertical migrations occur which might influence their distribution in a horizontal direction. Laboratory observations indicate that the larvae of *Ostrea edulis* do not swim continuously, but alternate swimming with short periods of rest, during which they sink down, either with expanded velum (0.4 cm./sec) or with closed valves (0.8 cm./sec.). Swimming is usually resumed well before they have fallen as much as 50 cm. (Korringa, 1951e). Extensive field observations carried through in the Oosterschelde with its strong tidal currents and thorough mixing of the water, which prevent stratification, failed to reveal any clear-cut vertical migration by the larvae of *Ostrea edulis* (Korringa, 1941a). The vertical distribution of larvae of all age groups appeared to be virtually the same at all hours of day and night, in any type of weather, and during all stages of the tidal cycle. There is certainly no tendency to sink down when the current exceeds 100 cm./sec. Since the larvae do not perform any vertical migration in the Oosterschelde, they will be at the mercy of the tidal currents and have no means of avoiding being swept out of the Basin. Observations on the horizontal distribution of the larvae fully confirmed this view. Larval distribution paralleled the data provided by our hydrographers so closely that oyster larvae could almost be used as an indicator for the origin of the water.

Similar results have been obtained by Loosanoff (1949b) on the larvae of *Gryphaea virginica* in Long Island Sound. He found no general relation between the vertical distribution of the larvae and the tidal cycle, and there was no evidence that larvae in advanced stages of development were more common near the bottom. The larvae do not descend to the bottom during periods of rapid tidal flow, and are as a result widely dispersed by the tidal currents.

The fact that oyster larvae often settle in great numbers upstream from the beds where the parent oysters live, though there is a general tendency to be swept downstream under estuarine conditions, has led to the hypothesis that the larvae can migrate upstream by descending to the bottom during the ebb. I have never understood how a certain group of larvae, swimming in a certain body of water, can distinguish whether it is ebb or flood. It is true, factors like salinity may change in the course of the tidal cycle at a given station, but the planktonic larvae move along with the water and do not stay as such a given station.

Carriker (1946, 1951a) made an effort to prove that the larvae of *Gryphaea virginica* may, especially in advanced developmental stages, move upstream (by remaining in the fastest currents on the flood and sinking down on the ebb) farther than can be accounted for by passive tidal conveyance. He carried through extensive series of quantitative

sampling from a boat anchored in Barnegat Bay and Great Bay (N. J.). In the former water especially hydrographical conditions appeared to be highly complex. Considerable differences in salinity and current velocity could be observed at short distances in both vertical and horizontal directions. As might be expected under such conditions the larvae of all stages did not flow past a given point uniformly distributed, but were very unequally spaced, both in a horizontal and in a vertical direction. Sometimes there was a rather gradual increase or diminution, and at other times the larvae apparently occurred in pockets, like clouds in the sky. Unfortunately, Carriker found that the larvae in advanced developmental stages were not common and eyed larvae were even rarer. The greatest larval concentration did not show a constant distribution with respect to the halicline in Barnegat Bay. In Great Bay the water appeared to be more thoroughly mixed, so that no haliclines were found there. From Carriker's numerous data I deduce that horizontal movements of the larvae predominate. The horizontal distribution of the larvae being very unequal in the different water layers, it seems impossible to draw conclusions on their vertical migration. Only continuous sampling from a given group of larvae would make it possible to study vertical migration, to which end it would be necessary to sample from a boat floating along at the same speed as the water layer in which the larvae occur; and even then it would be advisable to try to follow the movements of easily recognizable larvae by using a method of vital staining, like that described by Loosanoff and Davis (1947).

With the best will in the world I cannot deduce from Carriker's data that his oyster larvae in any stage of development tend to travel into the headwaters of the estuary by performing rhythmical vertical migrations. Is it not a too highly generalized picture of the hydrographical conditions in an estuary which makes it impossible to explain the setting of oysters in the headwaters in terms of passive tidal conveyance alone? The reality is certainly very complex indeed, and though there is undeniably a general tendency for downstream water movements, setting may occur upstream if even a very small percentage of the larvae find themselves carried upstream at the end of their pelagic life.

Of quite a different character are the vertical migrations of the larvae of *Ostrea edulis* as observed by Cole and Knight Jones (1949a) in the Conway rearing tanks and in Helford River (Cornwall). They found that larvae of all age classes tend to concentrate in deeper water layers during periods of bright sunshine, and have reason to assume that some factor associated with photosynthesis is involved in this phenomenon. A more even distribution of the larvae was found on dull days. Apparently this phenomenon is restricted to clear and rather quiet waters, for no evidence of this nature could be obtained in the rather turbid Oosterschelde with its powerful currents and thorough water mixing.

XIX. SETTING

"The most critical phase in the life history of the oyster is the period of settlement. The fact that the sensory equipment and vigour of the larvae reaches its highest development immediately prior to settlement is no doubt correlated with the importance of the choice in ensuring survival" (Cole and Knight Jones, 1949a).

We should, however, not presume that the inborn behavior pattern of the settling larva safeguards it from making serious mistakes in choosing a site for its future sedentary life. Needler (1941a), for instance, observed frequently that the heaviest set of spat of *Gryphaea virginica* occurs in Canadian waters in a shallow zone where the oysters are in serious danger of being killed in winter. This phenomenon could be explained by the fact that clean surfaces are especially abundant along the shore where wave action constantly washes the silt away from the prospective collectors.

Many experimental observations on the setting of the larvae of *Ostrea edulis* under natural conditions have been carried out in the Oosterschelde (Korringa, 1941a). Among other things, it was found that the larvae prefer to settle down with the umbo of the shell pointing in a very definite direction, irrespective of the angle at which the collector is placed, provided that the latter is not placed precisely horizontal. The pull of gravity is no doubt involved in this phenomenon. Of great practical importance are the calculations on the number of larvae settling in the Oosterschelde. Though many collectors are placed by the oystermen (several millions of tile collectors and over 10,000 M^3 of mussel shells annually), convincing evidence can be adduced that only about 1 per cent of the mature larvae are able to find these collectors and to settle down on them. All the others perish because they fail to find a suitable collector at the right time. By far the greater part of the

bottom and shores of the Oosterschelde is an uninhabitable desert for oyster larvae. Searching for a piece of collector free from silt in the 600,000,000 M^3 of water contained in the Basin of the Oosterschelde is to the tiny oyster larvae like looking for a needle in a haystack. And even of the larvae which are so fortunate as to settle, about nine out of ten perish before winter comes, through silting, through a too rapid growth of stronger organisms, and through the voracity of starfishes. The *number* of mature larvae per unit volume of water appears to be a good measure of the intensity of future settlement, and thus can be used with greater accuracy in predicting setting than the so-called "fixation-coefficient," indicating what *percentage* of the larvae is mature at a certain moment (Lambert, 1946b). In years when there is a large population of adult oysters a warm or fair summer always leads to a good set in the Oosterschelde, a cold summer to a poor set. Light did not appear to be a factor of major importance in the setting of oysters in the rather turbid Oosterschelde, and neither did the color of the substratum appear to exert an appreciable influence. Currents are certainly of very great importance in the setting of oysters under natural conditions. They transport the larvae to and in between the collectors, which are often successfully placed far away from the mother oysters. On the other hand, strong currents do prevent the larvae from settling. Ample evidence could be adduced that shelter from currents greatly influences the intensity of setting, and that most of the setting is concentrated in the periods of slack water. The angle of the surface of the collector is also of importance, vertical surfaces being less suitable than those exposed at any other angle. Contrary to general experience, oyster larvae appeared to settle profusely on the upper horizontal surfaces of the experimental collectors placed in the Oosterschelde, at least in stations free from silting. Survival and growth is usually best on under surfaces, as the danger of silting and algal growth is very limited there.

In experiments on the vertical distribution of oyster spat it was consistently found that setting is by far the best close to the bottom. Floating collectors caught very little spat in the swiftly flowing water of the Oosterschelde. The mature larvae being rather evenly distributed in the water, this phenomenon is explained in terms of current velocity, which is greatly reduced near the bottom. Similar results have also been obtained by Cole and Knight Jones (1949a) in Helford River and by Loosanoff and Engle (1940) when investigating the setting of *Gryphaea virginica* in Long Island Sound. Irrespective of the place where the latter installed their experimental collectors, they found that the heaviest setting occurred near the bottom. This contrasts with the results of Mackin's experiments (1946), for he found in the waters of seaside Virginia the heaviest setting from 1 to 2 feet above mean low tide level, and counted only a negligible number of spat below it. Mackin offered no explanation for this phenomenon. Did no larvae settle in the deeper layers, owing to very special hydrographical conditions, or did they fail to survive? McDougall (1943), who studied the setting of sedentary invertebrates in the Beaufort area, found that considerably greater numbers of oyster larvae settled on his artificial collectors below low tide level than on those placed in the intertidal area. Very soon, however, the spat which settled below low water mark showed such a heavy mortality that very few survived, so that ultimately almost all the spat was found in the intertidal zone. If Mackin's findings are to be explained in terms of such a differential death rate, the mortality must have struck very soon after setting, for Macking made some of his counts of spat only 4 weeks after placing his collectors. Loosanoff and Engle further observed that the setting was most abundant when the depth was 5 to 10 feet, and poor when it was 30 feet or more. They calculated the losses during the first few months of sedentary existence at 86 to 100 per cent, for which they mainly blamed the voracious starfishes. Factors like silting, algal growth, rapidly growing sponges, and ascidians are not mentioned in this connection.

Thomson (1950) studied the pattern of distribution of spat of *Gryphaea commercialis* (Australia) on cultch material set in various ways. He approached the problem from the practical side, however, counting the spat almost a year after placing the collectors. The use of this method makes it unavoidable that factors affecting the survival rate may have influenced the figures collected. Upper horizontal surfaces especially, heavily silted and covered with algal growth, showed low figures. Thomson placed his fibro-cement slats in several different ways, and found that the setting was better when the slats were placed ½ inch apart than when placed 1 inch from each other. Apparently shelter from the force of the currents, threatening to wash the settling larvae away, was here too a factor of great importance. This can also be deduced from Thomson's observation that

the middle sections of the collectors bore more spat than the end sections. The peculiar horizontal distribution of the spat on the different slats placed in a row is also very suggestive in this respect. Comparison of setting on slats placed with their broad surface horizontally with those having their broad sides placed vertically indicates that vertical surfaces are less suitable to setting of *Gryphaea commercialis* than are horizontal surfaces, exactly as in *Ostrea edulis*. Thomson stated that low catches on upper surfaces could perhaps be interpreted as a result of the settlement of silt, but he has also suggested that the construction of the containers I used in the Oosterschelde may have caused the high figures for upper horizontal surfaces there, because current swirls might have upset the natural orientation of the larvae in the water. Similar remarks have been made by Cole and Knight Jones (1949a), who, like Wilson (1941) found that the larvae in tanks settle by preference on under surfaces. In contrast to open waters, silting is a negligible factor in tanks. The prevalence of horizontal over vertical movements in open water, in sharp contrast to tank conditions, makes us still hesitant to assume that oyster larvae have a natural preference for undersurfaces as Cole and Knight Jones believe, for factors like the swimming behavior of the larvae, the accessibility of the collectors, and perhaps light certainly are very different in tanks and open waters. We are continuing our field experiments with a new type of collector which prevents swirling, and hope to present our data before long.

Cole and Knight Jones (1949a) described two entirely new and very interesting aspects of the settlement of oyster larvae. First, the occurrence of gregariousness in settling. More spat appeared to settle on collectors which already bore some spat than on those without spat. If this early spat was, however, killed with a hot needle, it appeared to lose its attractiveness for the spat settling later. This gregarious tendency can be of great importance for many sedentary organisms and presumably is a much more widespread phenomenon than is so far known. I have now collected experimental evidence myself on gregariousness in the setting of oyster spat in the Oosterschelde, and hope to publish my data soon. The other important finding is the noteworthy observation, corroborated by a series of experiments, that perfectly clean surfaces are less attractive to oyster larvae than so-called prefouled collectors, bearing besides some bacterial and diatomaceous film, some hydroids and other sedentary organisms To remain attractive to the settling larvae, the cultch should, however, be free from silt (which it is in the rearing tanks), and cultch placed too early and covered with too many organisms appears to be a real death trap for the larvae instead of being especially suitable for settlement.

Knight Jones (1951), who studied the setting of *Ostrea edulis* on Essex oyster beds, found that upper surfaces are unfavorable for setting there. He used experimental collectors of special construction to avoid turbulence, but admitted that some silt collected on the upper surfaces, which may have interfered with his results. Knight Jones corroborated the observations of oystermen who have found more spat on collectors placed on well-stocked oyster beds than on collectors planted on barren grounds. He has explained this in terms of gregarious settlement, assuming that gregariousness is perhaps associated with olfactory responses to some waterborne secretion of the older oysters. Though I agree with Knight Jones that more spat may settle on collectors on well-stocked beds than on those placed nearby on barren grounds, I do not believe that this can be explained in terms of gregariousness in settling and of the influence of some olfactory response, since the water currents are swift and rapidly disperse any possible waterborne excretion, while the tiny oyster larvae have very little chance of swimming against a gradient. I have new experimental data to support my view, but this is not the place to present them.

XX. NATURAL BEDS

Thriving natural oyster beds are of exceptionally great interest for studying reproduction and survival under completely natural conditions. Though natural beds of *Ostrea edulis* once fringed much of the Europaean coastline (Lambert, 1946a), the remains found nowadays are very scanty indeed (Dalido, 1948). There is virtually but one really flourishing natural bed left, and that is peculiarly enough the youngest of all, the Limfjord oyster district in Denmark. Oysters were found to spread here in 1850, about 25 years after the breaking through of the isthmus which formerly separated the Limfjord from the North Sea (Spärck, 1951). The stock of Limfjord oysters has shown considerable fluctuations. Periods of increase (1860–1870 1900–1914) alternated with periods of decline (1880–1890, 1914–1932). From 1925 to 1937 all fishing was suspended on account of the greatly reduced stock. Recent years brought a marked re-

habilitation of these natural beds. It is very interesting to learn that the recent increase started from the same small sheltered inlets and bays from which the oysters spread about 100 years ago, and also that rehabilitation is a slow process. A series of favorable years is necessary to produce a marked increase in the stock of oysters. Spärck (1950b, 1951) adduced convincing evidence that here, on the northern fringe of the range of *Ostrea edulis*, it is in the first place the water temperature during the warmest summer month which is decisive for success or failure in reproduction. Other factors probably are of minor importance here. Spärck has tried to explain fluctuations in the stock of oysters in several other European countries—farther away from the temperature limit for their reproduction—in terms of water temperature in the warmest month, and has even minimized the effect of the disastrous mortalities in the early twenties. One should, however, be very careful in estimating temperature conditions elsewhere in Europe from observations in Denmark. Several summers which favored oyster reproduction in the Limfjord were recorded as cool or even cold in Holland. That the period 1924–1930 had lower summer temperatures than the period 1937–1947 certainly does not hold good for the Oosterschelde (cf. Korringa, 1947a).

Though summer temperature is no doubt an important factor near the northern fringe of the oyster's range, other factors may be decisive elsewhere. We cannot accept, for instance, Storrow's (1947) assumption that climatical fluctuations may have been responsible for both the disastrous decline of the Scottish oyster beds about 1870 and the sharp increase of the stock of oysters in the Oosterschelde between 1870 and 1883, for he does not even mention the terrible and wasteful overfishing of the Scottish beds and the creation of a flourishing oyster culture in Holland at that time. The variety of factors which may determine the rise and fall of an oyster stock in places where man exerts his influence has been discussed in my paper on the vicissitudes of the Dutch oyster industry (Korringa, 1947a). Not only summer temperatures, but also severe winters, oyster diseases, competitors, the arrival of new pests, and both economical and political conditions have had a great influence. Newcombe (1950b) adduced evidence that silting, brought about by deforestation and improper use of the land, may threaten many formerly flourishing natural oyster beds in Chesapeake Bay. The silt piles up on many oyster bars and destroys the conditions essential to their existence by covering shells and other natural cultch material. Wasteful exploitation destroyed the once flourishing natural beds of *Ostrea lurida* in Willapa Bay (Kincaid, 1951).

That most of the natural beds of *Ostrea edulis* disappeared through serious overfishing and wasteful exploitation is generally accepted (Dalido, 1948), but it is not always readily understood why no revival came when fishing was suspended for a longer period. Hagmeier (1941) described the serious decline of the German natural oyster beds and the disappointing results of the efforts to revive them by relaying a fair number of French and Dutch oysters. He concluded that the latter probably belong to varieties of *Ostrea edulis* which cannot thrive and reproduce in the German Wattenmeer. According to Hagmeier, only the genuine German oyster, and perhaps some oysters of northern origin, can be used for a revival of the German natural beds. He suggested concentrating the few German oysters left on a small plot in order to increase the chance of fertilization, and expects such a spectacular revival that oysters may become a cheap popular food in Germany. Gross and Smyth's considerations (1946) are of the same nature. Taking into account the large number of larvae each oyster can produce, and rejecting the suggestion that considerable climatic and hydrographical changes make a revival of the natural beds impossible after a period of overfishing, they concluded that something must be wrong with the oyster itself. They assumed that the remaining scanty populations are now genetically too uniform and have lost their evolutionary plasticity. They suggested promoting mass hybridization by relaying oysters of different origin and expect then a general revival of the once flourishing natural beds. Orton (1946) rightly remarked that such a mass hybridization certainly has had its chance, for many foreign oysters have been relaid in the Thames estuary without leading to a revival of the local natural beds. According to Orton, the provision of a really large central spawning stock may be a better remedy than bringing in small quantities of oysters of different origin.

I discussed the fate of seriously overfished oyster beds myself (Korringa, 1946a, b), and explained why a general revival does not usually follow the suspension of fishing. Data collected in the Oosterschelde demonstrate that only a small percentage of the larvae reaches the setting stage,

and that very few indeed of those mature larvae succeed in finding a suitable collector, even in the Oosterschelde, where so many artificial collectors are provided. Even on natural beds where the overwhelming majority of the larvae are not swept away to districts unfavorable for survival and setting, the chance of finding a good collector is very limited indeed. Overfishing not only brings about a serious reduction in the number of parent oysters—and thus in the number of larvae produced—and not only destroys innumerable young oysters attached to the valves of the marketable oysters, but also leads to a very serious reduction in the number of suitable collectors available, since the most natural collector is the clean growth rim of the adult oyster shell. This cumulative effect of serious overfishing makes a revival very difficult. If beds are so seriously understocked that fertilization becomes incomplete, the beds will disappear completely. Spärck's data (1951) clearly indicate that even in the well-sheltered Limfjord, where the larvae can hardly be swept away by the currents, rehabilitation of natural oyster beds requires many years, even when all fishing is suspended.

Dannevig (1951) and Gaarder (1950) have recorded that several flourishing natural beds once existed along the Norwegian coast, but that very few "wild" oysters can be found nowadays. Overfishing meant that one took away the capital itself instead of the interest only, and the few oysters left over were not able to reproduce the stock in this northern area where water temperatures greatly limit the possibilities of reproduction. The old natural bed near Heligoland (Germany) is practically extinct now. Caspers (1950) has deemed it probable that even in earlier times this bed could hardly be considered as self-supporting. Oyster larvae brought in by the currents from more densely populated areas settled there on clean shells and on the valves of older oysters. The larvae produced locally had a very poor chance of remaining in the vicinity of the bed until they were ready to settle. In the last few decades very few young oysters could be found on the Heligoland bank. Too few larvae arrive here now from other districts.

Ranson's view (1943) that only natural oyster beds can ensure the reproduction of the stock seems rather odd when we compare the few very scanty remains of natural beds of *Ostrea edulis* with the thriving oyster industries in France and Holland. Lambert's view (1946a) that the scanty remains of some French natural oyster beds can only eke out their existence because they receive some mature oyster larvae from the millions of cultivated oysters grown on nearby parks, seems more plausible. Recently Ranson (1951b) explained in greater detail what he means when he says: "Les huîtres des bancs naturels sont seules susceptibles d'assurer la perennité de l'espèce." He does not mean that only "wild" oysters living on natural beds can produce offspring. The thriving and self-supporting oyster industries in the Oosterschelde and in the Basin of Arcachon are there to demonstrate that cultivated oysters may reproduce very well. Ranson only wants to express his view that conditions favorable for larval development occur only locally, and that such conditions may be expected practically exclusively in sites where natural oyster beds are found. The culture of oysters in the Oosterschelde and in the Basin of Arcachon is so successful because it has been established in waters where natural beds existed earlier. Millions of oysters may, on the other hand, be relaid for growth and fattening in districts unfavorable for larval development, and no setting will ever occur there. There are certainly many places where the larvae are carried away by the currents, or where they fail to find sufficient food. We have discussed in previous sections whether or not salinity too has, as Ranson has claimed, a direct influence on setting.

We agree with Ranson's view that many places where oysters are relaid for growth and fattening are not suitable for larval development, and that natural beds indicate where larval development is possible. We should add, however, that it is often possible in places where oysters do not occur naturally for other reasons. Collectors can often be placed with success in sites where bottom conditions prohibit a natural setting of oysters, for instance in many muddy inlets in the Morbihan (France) and in the Norwegian oyster polls.

(To be concluded)

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

REVIEWS AND BRIEF NOTICES

General Biology: Philosophy and Education 309
Biology: History and Biography 309
Ecology and Natural History 314
Evolution 315
Genetics and Cytology 316
General and Systematic Botany 316
Plant Physiology 319
Economic Botany 320
General and Systematic Zoology 321
Economic Zoology 321
Animal Morphology 323
Animal Physiology 324
Animal Nutrition 325
Biochemistry 326
Health and Disease 328
Psychology and Animal Behavior 330
Human Biology 335
Biometry 336
De Omnibus Rebus et Quibusdam Aliis 336

GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

AN OUTLINE OF GENERAL BIOLOGY. *Sixth Edition. College Outline Series.*

By Gordon Alexander. Barnes & Noble, New York. $1.00 (paper). xiv + 219 pp.; text ill. 1951.

This type of outline and summary of essential biological facts is frequently useful to students who are unable to digest the standard college textbooks for themselves. The *Outline* is quite accurate but is even farther behind in reflecting the changing viewpoints and emphases in biology than the textbooks themselves. The author has provided page references to most of the standard textbooks including those published or revised in 1950 and 1951.

BASIC EXERCISES IN COLLEGE BIOLOGY.

By James A. Dawson and William Etkin. Thomas Y. Crowell Co., New York. $2.25 (paper). viii + 232 pp. + 1 pl.; text ill. 1951.

This well-organized and attractively illustrated laboratory guide emphasizes the morphological study of representative plants and animals.

CELLULA. *Part 4. Tabulae Biologicae, Vol. XIX, Part 4.*

Edited by H. Handovsky; systematic register and subject index arranged by the Editor. Dr. W. Junk, The Hague, Netherlands. G. 15.00 (paper). vi + 68 pp. 1951.

This is the extensive index by subject and species to the 18 papers which have appeared since 1939 in the 3 issued parts of *Cellula*.

BIOLOGY: HISTORY AND BIOGRAPHY

PARACELSUS—*Magic into Science.*

By Henry M. Pachter. Henry Schuman, New York. $4.00. xvi + 360 pp. + 12 pl. 1951.

This commentary on the life and thought of Paracelsus is a sensitive personal study, not without considerable charm and interest. Unfortunately, its presentation is repetitious and episodic, as a whole it does not flow, and it is rather long on medieval philosophy and short on objective facts. One gets more of an impression of the things Paracelsus talked about than of what he actually said.

Pachter feels that "each generation must rewrite its history books in the image of its own experience.... Our attention turns to the historical failures, to those

who lived in the dark or who were crushed between the millstones of reaction and revolution in their time." This implication seems to very incompletely characterize the vigorous Paracelsus, who lost many battles, but not, in any significant sense, the last. Indeed, Paracelsus' embroglios are actually described as having nothing to do with upper and nether millstones, but to be quite directly a result of his magnificent maladjustment to contemporary corruption and pseudo-medicine, combined with a knack for not keeping his friends, a prodigious conceit, and a repeated evasion of contracts.

Pachter does reassert the universality of Paracelsus and the importance of his thought as one of the great independents who broke a way out of the thickets of medieval superstition and energetically groped toward points of view prerequisite for modern biochemistry and medicine. A lack of integration detracts from but does not obscure a really interesting presentation of a man deeply compassionate toward humanity and bitterly impatient with its individual specimens, a supersensitive iconoclast, a lonely master of invective who was hounded by contemporary physicians for many reasons, inter alia that he scorned academicism, compounded his own prescriptions, wrote in German instead of Latin, was not above assisting women in childbirth, and wrote a book on surgery which "described no operations but concentrated on how to avoid them . . . the only one of his major works printed during his lifetime." The tragedy of his personal relations is epitomized by an occasion when, after caring for the sick during an outbreak of plague, he was ordered by the citizens to leave town after the plague had been halted.

EVELYN HOWARD

JOHN WILLIAM DRAPER *and the Religion of Science. By Donald Fleming. University of Pennsylvania Press; Geoffrey Cumberlege, Oxford University Press, London.* $2.50. x + 205 pp. + 1 pl. 1950.

John William Draper (1811–1882) was an interesting and versatile member of what has been for some time an interesting and versatile family. His early training was in chemistry at University College in England and in medicine at the University of Pennsylvania; he was an investigator whose research lay in the fields of photochemisty and of the applications of physics and chemistry to biology; he made particular contributions to photography and spectroscopy. He was a teacher, first at Hampden-Sidney in Virginia and later as a member of the Medical Faculty at New York University. Both in his lectures and in his writing he was an ardent and assiduous popularizer. Midway in his life he turned away from the practice of science to other things, and early in the 1860's he published a three-volume *History of the American Civil War*, later in the decade *A History of the Intellectual Development of Europe*, and in 1874 a *History of the Conflict between Religion and Science.*

The basis for a historian's interest in him is apparent, and this biography was written by an Albert J. Beveridge Memorial Fellow of the American Historical Association. It is extremely well-written; in fact, too well. Draper made no epoch-breaking contributions to science, but what he accomplished deserves a different kind of evaluation than that "most of his work with radiant energy is a monument to the virtues of the experimental method, which wrings useful observations from doubtful hypotheses." The author, furthermore, never comes fully to grips with what is to many the most interesting problem concerning Draper, namely, the conflict within him which diverted him from science to history: "when all of this is said, one has just nibbled at the edges of the question why Draper substantially ended his laboratory research by 1860 and never repented." The question that might be raised in this connection regarding the ability of the "historian" to understand the "scientist" may for the present volume be dismissed as irrelevant. The same difficulties arise in the author's treatment of more strictly historical themes. Is it not perhaps more clever than profound to comment that "Draper's science of history is therefore not unfairly to be described as the result of mixing up together Shakespeare's seven ages of man and Comte's three stages of thought"? And where in the volume is to be found the intellectual historian's exhaustive and critical evaluation of the influence of Draper's own intellectual history on the intellectual historians who followed him? To say that "*The Intellectual Development* is in this sense a kind of first draft of the last testament of the Age of Mazzini and Mill" is provocative but not sufficient.

Somewhere early in the biography the author describes the first of Draper's "long series of annual 'introductory lectures,' where the trick was to get up wind quickly for a plausible flight very high above the subject-matter of the course to follow." The reader has the uneasy feeling that in the biography, too, the writing is on a plane not coinciding with that which encompasses the content. The book, however, is an interesting commentary on an interesting mind, and will be read with particular edification by all who are interested in the scientific and intellectual history of the latter part of the 19th Century.

JANE OPPENHEIMER

STEVE MATHER OF THE NATIONAL PARKS. *A Biography. By Robert Shankland; introduction by Gilbert Grosvenor. Alfred A. Knopf, New York.* $4.00. xii + 326 pp. + xxii (index) + 25 pl. 1951.

For the reviewers, who have enjoyed the facilities at most of the national parks and national monuments for which Steven Tyng Mather worked so consistently

and effectively, this book brings to mind happy days and many friends in the National Park Service. It is crammed with the historic background of the 1915–1951 period, with the legal struggles and congressional moves that changed a haphazard assortment of independently administered public lands into a national pattern of parks and monuments, and raised the positions of superintendent and ranger alike to esteem and respect. Throughout the biographical account, it is clear that many of Mather's successes were due to his previous financial status, but the driving force that has worked so well in the national interest is just as obviously that of an outdoor man whose enthusiasm for scenery and wildlife knew few bounds. John Muir, who died broken-hearted over the Hetch Hetchy steal from the great Yosemite area, would have glowed and gloated if he could have followed these pages and seen how much came from the conservation movement he championed. It is Muir's torch that Mather carried. The product is a national heritage of which all can be proud.

LORUS J. & MARGERY J. MILNE

ECOLOGY AND NATURAL HISTORY

PHYSICAL GEOGRAPHY.

By Arthur N. Strahler. John Wiley & Sons, New York; Chapman & Hall, London. $6.00 x + 442 pp.; ill. 1951.

In this textbook, Strahler has attempted to present physical geography as a basic earth science unhampered by any relation to human or economic geography. Although reference to these other phases of geography must be made, they are subordinated to his main theme —that of presenting only the principles and techniques of geography as an earth science, in order to explain the processes and forms which develop on the land or in the sea or air. In general, the treatment of physical geography presented by Strahler is conventional, following the pattern set up by earlier scholars such as Salisbury and de Martonne. The author's desire to include and use newly developed principles and methods of presentation has led to the volume's publication at this time. How well the author has accomplished what he has set out to do may be seen by considering a few specific points.

The diagrams and illustrations used in the book, many by Lobeck, Raisz, and W. M. Davis, are exceptionally fine. Strahler has used far more diagrams and figures than previous authors and has selected them well to illustrate and clarify important points in the text.

In trying to incorporate newly developed principles in physical geography, the text has in places become no more than a glossary of terms. Many of the technical expressions used, while correct, appear to be suited more to a graduate level course. The text would have gained strength and clarity by a reduction in the number of technical terms and a more careful explanation of those used. The inclusion of a glossary in the appendix would have been helpful to beginning students.

There is a great need at the present time for a well-integrated laboratory course in physical geography. The exercises at the end of each chapter, constituting one-sixth of the book, offer an admirable foundation for such a course. The exercises include not only discussion questions, but also work on both topographic and meteorologic maps.

The author has failed to include in his presentation many important new geographical principles. This is especially true in fields other than the author's own, which is geomorphology. For instance, in evaluating precipitation on a basis for a climatic classification, Strahler employs a very inadequate scheme outlined by Blair. Pointing out its obvious limitations, the author comments that schemes which combine precipitation and temperature may give highly satisfactory results. In the last few years such a scheme has been developed and is now being widely applied, although no mention of it appears in the text. The scheme results in a greater appreciation of the moisture factor in climate through a comparison of the potential evapotranspiration water losses of a region with the available precipitation. In addition to providing a moisture index, potential evapotranspiration is an index of thermal efficiency. Thus, it is possible to relate the two most basic climatic factors, heat and moisture. Application of this scheme to the problems of climate will lead finally to a more realistic concept of physical geography itself.

The book is divided into three parts. The first section, which considers the earth as a globe, includes chapters on the form and illumination of the globe, map projections, the moon and tides, and time. The second section, in which planimetric and topographic maps and rocks, structures, and landforms are discussed, has chapters on weathering, mass wasting, landforms, horizontal strata, plains, folds, faults, and volcanic forms. Section three, on weather, climate, and soils, includes discussions of the geographic distribution of the various climatic parameters, the climates controlled by both arctic and tropical air masses, and the great soil groups.

Of the three sections, section one is the most adequate. Although Strahler belabors some of the points in this section and mathematical explanations and examples abound, the coverage is more inclusive, the diagrams are clearer, and the explanations more lucid than in previous geography textbooks.

The second section, except for the excellent diagrams and illustrations and the specialized geomorphologic vocabulary, is entirely conventional. The chapters on landforms made by wave action and streams are probably superior to the others in this section.

The third section, which as Strahler admits merely follows the work of Trewartha and others, is the weak-

est of the three. The discussion of the distribution of climate attempts to bring in the closely related problems of soil and the distribution of vegetation. Here the treatment becomes unsatisfactory. The discussion of the biotic factor is limited to a relatively few paragraphs, and its relation to climate and to soils is inadequately shown. Soils and vegetation cannot be separated from climate, and any integrated treatment must deal fully with all of the related problems.

Strahler has been only partially successful in his endeavor to offer a physical geography textbook which would incorporate new principles and methods of presentation. His attempt fails mainly because the scope of the field is too wide to be adequately encompassed even in a textbook by the knowledge of any one man.

JOHN R. MATHER

ZOOGEOGRAPHY OF THE LAND AND INLAND WATERS. *By L. F. de Beaufort. Macmillan Co., New York; Sidgwick & Jackson, London.* $5.00. viii + 208 pp.; ill. 1951.

It is extremely gratifying to have a European zoogeographer quote with approval Darwin's caustic remark about those "who make continents as easily as a cook makes pancakes." Darwin and Wallace, the founders of modern zoogeography, postulated that the continental platforms had been essentially stable throughout geological history. They believed that the terrestrial animal life of the globe had reached its existing distribution mainly by passage over a former connection of Eurasia and North America at Bering Strait; over the existing and formerly more varied connections of Africa with Eurasia; via connections of the East Indian islands; and over the existing "land bridge" at Panama; with this overland dispersal they combined a considerable allowance for trans-oceanic "accidental" dispersal.

In the latter part of the 19th century there grew up a school of "land-bridge" zoogeographers who believed that other connections between the existing continents, either of continental proportions or as narrow isthmuses, were required to explain every disjunct distribution. Australia was thought to have been connected with South America because hylid frogs and marsupial mammals occur mainly in these two regions. Africa was thought to be connected with South America to explain another set of relations. Madagascar and the peninsula of India were connected across the Indian ocean by the special continent "Lemuria" to account for the existing distribution of lemurs. Even the North Atlantic was bridged (in these zoogeographers minds) by a land connection to explain the existence of the moose in Canada and the elk in Norway. Indeed, a new land bridge hypothesis might be proposed to account for any disjunct distribution, even in a single genus of beetles.

When the data of physical geology accumulated to prove that the continents consisted of lighter rock masses floating on denser material, which latter also constituted the floors of the ocean basins, the multitude of imaginary connecting continents had to be given up. At this juncture the ingenious continental drift theory of Alfred Wegener seemed to save the day for the arguments regarding direct land connections of the southern continents, for this theory postulates that all of the continents were originally juxtaposed and reached their present isolated positions by drifting apart in the geologic eras since the Paleozoic. The rough correspondence of the continental outlines of the Atlantic coasts of Africa and South America were thought to be vestiges of their former intimate connection. The bridge-building zoogeographers let their oceanic continents drop back to the bottom of the sea and triumphantly espoused the Wegenerian alternative. Wegener himself had assumed that the data of animal geography require a hypothesis of land connections in the southern hemisphere.

The only factual and positive evidences in historical animal geography are the data of paleontology. When W. D. Matthew in his essay *Climate and Evolution* in 1915 synthesized the accumulated evidence concerning the Tertiary evolution of mammals, he was able to present overwhelmingly cogent arguments to prove that the past and present distribution of this great group could be accounted for by the few immediately evident intercontinental connections. Even more important, perhaps, was his demonstration that other hypotheses of land connections to explain animal distributions, whether ante or post Wegener, introduced far more complications than they explained.

Matthew's method of thought, which was no more than a return to the Law of Parsimony and a turning away from uncontrolled fantasy, attracted a number of the younger American zoologists, some of whom have been veritable disciples. They have long been aware, and dismayed, that many of their colleagues 'knew not Matthew.' *Climate and Evolution* was long out of print, until a handsome reissue by the New York Academy of Sciences made it again available.

It has seemed necessary to offer this introduction to a review of de Beaufort's small text on animal geography because the author does not (even after the good beginning with the pancake quotation) convey to the reader any idea of the vital and radical differences between the two schools of zoogeographers, or anything of the excitement of the battle between them. He does indeed quote Matthew and reject some popular hypotheses of land connections, and he takes a rather dim view of continental drift; but elsewhere he adheres to the idea of tongues of land connecting the southern contents *via* Antarctica. De Beaufort cites three titles by G. G. Simpson, who is one of the most distinguished of the disciples of W. D. Matthew; but these prove to be by no means Simpson's most incisive discussions of the basic problem.

L. F. de Beaufort is professor of zoogeography at the University of Amsterdam. He is well-known as an authority on the fishes of the East Indies. It is accordingly appropriate that he has treated the connections of Britain with Europe, and of the Greater Sunda Islands with Asia and with each other, as examples of well documented "land connections." In a volume of only 184 pages, and with only 8 figures, not much more than an introduction to the subject is to be expected. Even so, for so small a work, there is too much of detail, and not enough of general principle, and, especially, not enough of illustrations with maps. Even the basic terms of animal geography are not defined, and the word *habitat* is still employed for what American students refer to as *geographic range*. *The Zoogeography of the Land and Inland Waters* devotes 9 pages to an introduction; 50 to the Holarctic Region, with a special chapter for the British Isles; 32 to the Oriental Region; another 32 to the discussion of the faunas of Africa and Madagascar; 22 to tropical America; and 32 to Australia and the Pacific Islands. A final chapter gives an account of the transition region between the Malaysian Islands and New Guinea and Australia, whose problems and inconsistencies have been a favorite topic of discussion and argument among zoogeographers since the time of Wallace.

De Beaufort is scarcely to be held responsible for details of English in this book, and his language is never especially obscure. The editors of the series of Textbooks of Animal Biology, however, might properly have taken their duties seriously enough to have substituted more exact wording in many places and to have done away with discrepancies in spelling; and more than lip-service might be paid to Fowler in the matter of the which-clause. *Xeric* for the author's "xerophilic," and *cold-limited* for his "*cold-loving*" seem obviously preferable usage. The reader nowhere learns that the much cited Scharff did not at all believe in continental glaciation; nor is he informed that the work of M. M. Metcalf on the opalinid parasites is stated by Metcalf's own most able student to be quite unreliable. There is bad taxonomy as well as good, and there must be some evaluation of the authors and works cited. To treat Scharff and Metcalf on the same plane as William Diller Matthew and George Gaylord Simpson is at best naive.

An American reader will stumble over the statement that "forests were rarer [in North America] in older Miocene times than in Europe, and a forest fauna comparable to and as rich as the European does not exist." The fauna and flora of southeastern North America are vastly richer than those of Europe, and must have been richer throughout the Tertiary.

Historical zoogeography has not had an adequate book-length treatment since Wallace's. A thoughtful and critical work, to which a rather full account of the land connection controversy would lend a lively interest, is greatly to be desired. De Beaufort's book is not the work in question, though it has real value for its summary of the faunal relations of the British Isles with the European continent and of the connections and separations among the great continental islands of the East Indies.

KARL P. SCHMIDT

THE LIFE OF THE SPIDER.

By John Crompton. Houghton Mifflin Co., Boston. $3.00. 254 pp.; ill. 1951.

Since most people display a fear or hatred of spiders, the naturalist welcomes worthwhile books that attempt to dispel these feelings. Using the literary techniques of the journalist, Crompton has written his book in a popular fashion and with this aim in view. There is no doubt that his enthusiasm will be communicated to the general reader, who will thus feel less revulsion for spiders and perhaps may even become an admirer. The book contains much that is praiseworthy. But it is regrettable that the author was not able to avoid the usual pitfalls in the path of the popular writer, such as anthropomorphism, generalization, the perpetuation of legends which have repeatedly been proved untrue, misrepresentation, and readability at the expense of accuracy.

The original printing of this book appeared in England in 1950 under the title, *The Spider*. The text of *The Life of the Spider* is identical with the British work except for the addition of an Introduction, a few titles to the literature list, and some footnotes intended primarily to make the book more valuable to American readers. Practically all of the great deal of information to be found in this work is based on the writings of others who actually studied spiders, and mixed with it are the author's philosophical thoughts and his own (sometimes false) interpretations. To the expert it is plain that Crompton has read only a rather small part of the literature on spiders. He leans most heavily on Bristowe and on Fabre, devotes an entire chapter to the latter. Some readers may find themselves irritated by lengthy, irrelevant asides. Others may find the verbosity tiring.

It is to his credit that Crompton abhors the adjectives "dirty," "repulsive," and "ugly" when used by others in alluding to spiders, but it is hard to reconcile this viewpoint with his own frequent use of "stupid," "cruel," "savage," "reprehensible," and "hard-hearted" in describing them. He warns his readers about generalizing and correctly points out that despite Fabre's account of a *Lycosa* which carried her spiderlings for 6 or 7 months it is nevertheless a fact that British wolf spiders may carry theirs for only 2 or 3 weeks. But again, how are we to reconcile this with his own erroneous generalizations, such as that all male spiders are incapable of spinning snares; that females almost always eat their mates; that crab spiders select flowers to match

their own coloring and that they are the most devoted of all spider mothers; that egg sacs are provided with a hard outer covering to keep out insect enemies; and so forth.

In several places Crompton repeats the incorrect statement that spiders merely suck blood, e.g., "It is blood she wants, not meat" (p. 32). Yet he correctly recounts from McKeown the manner in which a spider can digest solid portions of its prey before swallowing. One wishes that the author had been more consistent! Confusion also results from expressions such as "average spider," "live corpses," and "unspiderlike shape." His concept that the mating of spiders represents an "artificial insemination" is unfortunate. Another indication of the author's disdain for precision is given by his substitution of the term "smell" for the more precise term "chemotactic sense," which he considers difficult to pronounce. Moreover he implies that Doleschall and DeGeer were Americans, while in point of fact they were Hungarian and Swede, respectively.

In certain places Crompton indicates by footnotes that a particular species being discussed may also occur in the United States, or else he gives the name of the related species. Because of his admitted abhorrence of classification these footnotes sometimes incorrectly refer to entirely unrelated species. Moreover, although he dwells at length upon the changes in name of British spiders there is no attempt made to bring up to date the names used by Peckham in 1889. And while accounts are supplied of the bolas spiders of Australia and South Africa, it is regrettable that not even a footnote is given concerning the American species with similar habits, which were made known originally in 1903 and reviewed in a well illustrated popular article by Gertsch several years ago.

Throughout the work Crompton suggests explanations for phenomena in an anthropomorphic manner. In fact, he admits to being "unashamedly" so (p. 174). He accounts for the evolution of the pitcher plant spider by assuming that the spider "came to realize" it was on to a good thing, and that it later even developed a hard outer covering in order to resist the action of the plant's juices. For those interested in the evolutionary process he offers this aside concerning the sense of sight in man: "In the case of the animal, man, who uses the sense of sight more than any of the others, a strange phenomenon is taking place—the sense is deteriorating. . . . Now nature usually rewards the continued use of a member by improving that member and punishes neglect in the opposite way. . . . That is why domestic hens cannot fly and seals cannot walk and why we cannot recognize our friends in the dark by their smell. By right we ought to be able to demand from nature increasingly efficient eyes. . . . She *will* give us even better eyes, but only in her own time. And not if we wear spectacles. . . . I am not suggesting that we discard spectacles for the sake of our remote progeny."

This book is a curious admixture of good and bad in which the author has assembled much interesting information and has presented it vividly. In this review more emphasis has been placed on the faults, since they are more likely to escape the casual reader than are the creditable features.

B. J. KASTON

INSECTS IN YOUR LIFE.

By C. H. Curran. Sheridan House, New York. $3.50. 316 pp. + 16 pl.; text ill. 1951.

Since there are "five times as many species of insects as there are all other creatures put together," another book on insects is always helpful. The author of the present volume is a distinguished entomologist, Curator of Insects and Spiders of the American Museum of Natural History. In this, his first non-technical book, he writes simply and entertainingly. It is natural that he should start with his favorites the flies, but his taste is broad and he has included such various subjects as insects in the house, termites, Japanese beetles, and butterflies. He has a way of making attractive all sorts of information about the insects we meet most frequently, or want to know more about. He uses a light touch with such topics as the mystery of butterfly migration, tells of the work done in conjunction with the Sperry Gyroscope Company on the way a fly flies, and enters humorously into the problem of winter prediction from the bandwidth of the woolly bear caterpillars. More serious matters include the questions: Why is a carpet beetle on my rug? How can I get rid of clothes moths? What insects attack plants and animals? What is DDT? ("The Atomic Bomb of the Insect World.")

The spectacular has its place too: Four-inch grasshoppers that feed on mice, and walkingstick insects a foot long—both from Africa. One learns that the ancient Aztec observed "ants that grow in warm countries and destroy the trees and whatever there is . . . walk in flocks like people at war." Only the chapter on insects from Barre Colorado Island and Panama falls below expectations. Surely the blue irridescent Morphos —so thrilling a sight on the island—should have been mentioned, and the variety of colonial bees and wasps made famous by Phil Rau. Of course there is not space for everything. In connection with the gyroscopic action of the flying fly there are some excellent photographs and diagrams illustrating the connection to aerodynamics. Many of the other illustrations have a more textbookish style than one expects in an account of the natural history of insects. Large print assists the reader.

LORUS J. & MARGERY J. MILNE

NATURAL HISTORY AND ECONOMIC IMPORTANCE OF THE MUSKRAT IN THE ATHABASCA-PEACE DELTA, WOOD

BUFFALO PARK. *Wildlife Management Bull., Ser. 1, No. 2.*

By W. A. Fuller. Department of Resources and Development, National Parks Branch, Canadian Wildlife Service, Ottawa. Free upon request (paper). 82 pp. + 16 pl. March 1951.

WATERFOWL AND RELATED INVESTIGATIONS IN THE PEACE ATHABASCA DELTA REGION OF ALBERTA, 1949. *Wildlife Management Bull., Ser. 2, No. 2.*

By J. Dewey Soper. Department of Resources and Development, National Parks Branch, Canadian Wildlife Service, Ottawa. Free upon request; paper. 63 pp. + 9 pl. May 1951.

SHOAL-WATER GEOLOGY AND ENVIRONMENTS, EASTERN ANDROS ISLAND, BAHAMAS. *Bull. Amer. Mus. nat. Hist., Vol. 97, Art. 1.*

By Norman D. Newell, J. Keith Rigby, Arthur J. Whiteman, and John S. Bradley. American Museum of Natural History, New York. 75 cents (paper). Pp. 1–30 + 8 pl. + 1 folding figure; text ill. 1951.

EVOLUTION

CREATIVE ASPECTS OF NATURAL LAW.

By R. A. Fisher. Cambridge University Press, New York and London. 50 cents (paper). vi + 23 pp. 1951.

In this very brief lecture, R. A. Fisher undertakes to reevaluate Bergson's "évolution créatrice" and Smuts' holism. Both these theories see in life a creative, effective causation outside of matter and energy. This is of course inadmissible in a deterministic universe, but with the establishment of physical indeterminism, so Fisher reasons, creative causation becomes real. The flaw in the reasoning of Bergson and Smuts was that they rested the creative causation of the evolutionary process on insecure grounds, the former on the magical efficacy of willpower—of Lamarckian desire; and the latter on the direction of minor mutations by some intrinsic tendency of the egg toward completeness or integration. The modern experimental study of evolution shows that the real seat of creative causation in evolution lies in natural selection—"in the actual life of living things; in their contacts and conflicts with their environments, with the outer world as it is to them; in their unconscious efforts to grow, or their more conscious efforts to move. Especially, in the vital drama of the success or failure of each of their enterprises . . . on the Darwinian view, by doing or dying." Selection is thus both creative and holistic. Fisher concludes by emphasizing that ". . . the activity of the human race will provide the major factor in the environment of almost every evolving organism. Whether they act consciously or unconsciously, human initiative and human choice have become the major channels of creative activity on this planet." How little we are prepared for this, how little we know what we do! Ecological studies and population genetics are not yet strongly supported nor flooded with enthusiastic recruits. But the voice of the prophet is always a voice crying in the wilderness. Eventually it must be heard.

BENTLEY GLASS

STAGES IN THE EVOLUTION OF PLANT SPECIES.

By Jens Clausen. Cornell University Press, Ithaca. $3.75. x + 206 pp.; ill. 1951.

Experimental taxonomy, which arose out of the union of the static techniques of classical taxonomy and the dynamic concepts of evolution, genetics, and ecology, has become a lucrative and forward-looking field of research. Initiated in the early 1920's by Turesson's concept of ecotypes, experimental taxonomy has been brought to its present well-developed stage largely through the remarkable studies of the team of Clausen, Keck, and Hiesey on ecological races of certain species of composites inhabiting our western Coastal Range. In the past, these studies have been embodied in full detail in the numerous publications of the Carnegie Institution of Washington; the present volume, based on the Messenger Lectures given at Cornell University, is a well-rounded, coherent condensation of the facts and hypotheses arising out of the work done during the past 12 years. It is quite clear now that, with the proper techniques, evolution in the higher plants can be investigated as a dynamic process, and that it is subject to experimental analysis. The principal emphasis in these lectures has been given to a consideration of the genetic analysis of the local population (ecotype) as the basic evolutionary unit from which divergence proceeds, followed by a less detailed examination of the evolution of higher taxonomic categories. The species has been found to have a genetic organization far more intricate than had been formerly assumed, and in spite of its apparent taxonomic "immutability" it is exceedingly rich in genetic variation. It is precisely this system which, while providing the checks and balances that make for stability in a taxonomic sense, also provide for an inherent flexibility and tolerance necessary to meet changing environmental conditions without danger of extinction. Together with Dobzhansky's study of the dynamics of *Drosophila* populations, Stebbins' reconstruction of species relationships in the Graminaceae, and Babcock's analysis of the cytogenetics of *Crepis*, the work of Clausen, Keck, and Hiesey has furnished a window from which we can view the changing evolutionary panorama with a clarity hardly considered possible a decade ago. For those who are unfamiliar with the more voluminous Carnegie reports, this volume provides an excellent and by no means fragmentary summary.

C. P. SWANSON

A NEW TITHONIAN AMMONOID FAUNA FROM KURDISTAN, NORTHERN IRAQ. *Bull. Brit. Mus. (Nat. Hist.), Geology, Vol. I, No. 4.*

By L. F. Spath. The British Museum (Natural History), London. 10s. (paper). Pp. 93–146 + 5 pl. 1950.

The stratigraphic position and zonal sequence of the Tithonian stage (Upper Jurassic) is still somewhat controversial. Every contribution concerning its stratigraphy and ammonoid faunas is therefore of highest scientific interest. In this paper Spath describes 20 species. No less than 16 of them are considered new, only 1 is identified with a previously described species, and a further one is attached to a known form. They are attributed to the genera *Oxylenticeras* n. gen. (subfamily Streblitinae), *Glochiceras, Pseudolissoceras, Phanerostephanus* n. gen. and *Nannostephanus* n. gen. (both subfamily Virgatosphinchinae), *Nothostephanus* n. gen. (subfamily Virgatitinae), *Proniceras, Protancyloceras,* and *Cochlocrioceras* n. gen. (family Protancyloceratidae). After an extensive review of the various Tithonian ammonoid faunas so far known, a tentative division of the Tithonian is established. The fauna from Kurdistan corresponds to the Meso-Tithonian, the Pseudolissoceras beds of this scheme. As in all the papers by Spath, the phylogeny and taxonomy of the described ammonites and of many related forms are amply discussed.

OTTO H. SCHINDEWOLF

MAMMALS OF THE REXROAD FORMATION FROM FOX CANYON, MEADE COUNTY, KANSAS. *Contrib. Mus. Paleontol., Univ. Mich., Vol. VIII, No. 6.*

By Claude W. Hibbard. University of Michigan Press, Ann Arbor. $1.50 (paper). Pp. 113–192 + 5 pl.; text ill. 1950.

Knowledge of the late Pliocene fauna of the Rexroad formation in Meade County, Kansas, is here extended through descriptions of 24 species of mammals, including 7 new species (2 insectivores, 1 bat, 1 rodent, 1 procyonid, 2 mustelids) and 3 new genera.

GENETICS AND CYTOLOGY

THE ORIGIN, VARIATION, IMMUNITY AND BREEDING OF CULTIVATED PLANTS. *Selected Writings of N. I. Vavilov. Chronica Botanica, Vol. 13, No. 1/6.*

Translated from the Russian by K. Starr Chester. Chronica Botanica Co. Waltham, Mass. Stechert-Hafner, New York. $7.50 (paper). xviii + 364 pp.; ill. 1951.

Nikolai I. Vavilov stands as a symbol of scientific persecution in a country where truth has been replaced by dogma, and where, outwardly at least, truth established through verification is no longer possible. His death during banishment brought his name to many who knew, and still know, nothing of him except that he fell from favor because of his genetic and evolutionary views. But Vavilov is to be remembered for much more than this. He was one of Russia's greatest biologists, honored and respected by his colleagues the world over. His papers on phytogeography, evolution, homologous variation, immunity to plant diseases, and wheat breeding are examples of prodigious effort, carefully marshalled evidence, and clearly framed conclusions and hypotheses. They are prophetic in what they point out, as well as being solid contributions for what they add to scientific fact and thought. They reveal a richly imaginative mind, a meticulous collector of data, an aggressive practical planner, and a man of action, one the world could ill afford to lose. He saw his science of plant breeding circumscribed by no national boundaries—"It requires the international spirit, the cooperative work of investigators throughout the whole world," he said—but he did not live to witness the utter negation of this philosophy. The present volume, containing some of Vavilov's better known papers, provides a fitting memorial to the man at the same time that it makes available to the English-speaking reader papers formerly printed only in the mother tongue. Biology owes a debt of gratitude to K. Starr Chester for his translation.

C. P. SWANSON

GENERAL AND SYSTEMATIC BOTANY

THE PLANT WORLD. *A Text in College Botany. Revised Edition.*

By Harry J. Fuller. Henry Holt & Co., New York. $4.75. xiv + 769 pp.; ill. 1951.

The issuance of the 2nd edition of Fuller's well known and apparently well received botany textbook does not mean that any marked revision of the text has been made. To be sure, information new since 1941 has been judiciously added, and new illustrations have served to lighten the burden of the text. The general tone and format remain the same. The greater length of this edition stems from lengthier chapter summaries (to lighten the burden on the student?) and the inclusion of review questions and references. It will take its place along with a dozen similar textbooks, no better and no worse than its companions, and, to any student other than a botany major, incredibly dull. All of which brings me to a subject in need of airing. General botany is not a subject for the botany major alone; the available textbooks, despite their introductory statements, belie this attitude, for the comprehensive treatment is far too detailed and technical, the role of botany in our society, including its cultural, economic, and evolutionary aspects, is inadequately handled and left for advanced courses, and an appreciation for good writing is rarely

noted. In view of the fact that the number of students preparing for a professional career in botany is extremely low compared to the number who embark upon a course in botany either through unfortunate choice or through the coercion of science requirements in our colleges, it is therefore remarkable that some author, gifted with a lively style, a sense of proportion, and an appreciation of plants that extends beyond the dried herbarium specimen and the stained scalariform tracheid, has not considered the preparation of a textbook which would present the plant world in all of its manifold wonders without the stultifying jargon which serves as a screen behind which the inadequate writer and the inarticulate teacher hides, and which, as deadly as cyanide, kills off the prospective and interested student before he has gotten a good taste of his subject. All too frequently the teacher must compensate for the deficiencies of his text, and not many are capable of doing this. A minimum of botanical jargon is, of course, necessary, but there is no logical reason, other than the 19th century traditions of teaching to which the writing botanists as a group so fervently cling, why botanical textbooks have set such a premium on literary dullness. Scientific accuracy and literary quality have not yet, to my knowledge, been proven incompatible—witness Rutherford Platt's *Our Flowering World* and Peattie's *Natural History of Trees*, or, in related fields, Glass' *Genes and the Man* and Rachael Carson's *The Sea Around Us*. A good beginning text in botany is urgently needed, and a financial killing awaits the gifted literary botanist. Ask any publisher. At the same time it is also recognized that it would be necessary to re-educate our teachers to make use of such a book, for the teachers are, in a sense, little different from the textbooks which they employ.

C. P. SWANSON

ALGAE OF THE WESTERN GREAT LAKES *Exclusive of Desmids and Diatoms. Bull. No. 31.*

By G. W. Prescott. Cranbrook Institute of Science, Bloomfield Hills, Mich. $10.50. xiv + 946 pp.; ill. 1951.

The author has spent a lifetime studying freshwater algae from Oregon to South America and New England, and including a very extensive study of the same organisms from the North Central States, the results of which form the present treatise. The author claims that his book is a compilation of all reports of freshwater algae for the region, but one suspects that his own observations far outnumber the purely compiled records. Forms other than those from streams, ponds, and lakes have been excluded for the most part. Unfortunately it was deemed also necessary to exclude the diatoms and desmids, since each of these would have required a similar volume by itself. It can be hoped that the major research interests of the author, the desmids, can be described in a companion volume, which would be desirable not only as a floristic study of the area for a group of organisms extremely important in the productivity of our water resources, but especially because there is no one better qualified to speak of American desmids at present than G. W. Prescott.

Following the usual introductory material is what might be called Chapter I, Geological Features and Algal Distribution, 30 interesting pages of limnology revealing something of the role of algae in the lakes of the area and their distribution according to soil types. The phytoplankton and lake productivity are treated in 16 pages, emphasizing physico-chemical factors and food chains, with a résumé of the factors that determine the character of lake floras. An interesting feature, consisting of 13 pages of illustrations, depicts the author's interpretations and applications of morphological terms. This precedes the Systematic Account (575 pp.). An analytical key to the genera, a glossary, a bibliography of 51 pages, 136 pages of figures, and an index complete the book. In the systematic account keys to the taxa are included down to the generic rank, whether the particular taxa are known from the Great Lakes area or not, unless only a very few taxa are concerned. The species included are those known or reported to the author from, largely, Wisconsin and Michigan. Of great welcome is the space-saving necessity of cutting the specific descriptions to the taxonomic essentials. The original place of description of each taxon is given. This book is preeminently a floristic treatment, and as a floristic treatment its coverage and detail, the proportion of species illustrated, and the keys command our respect.

The illustrations show some novel features unexplained in the text, e.g., Plate 80, fig. 5, shows the "oogonium" of *Nitella tenuissima* with a five-celled coronula, although *Nitella* species are believed to possess, uniformly, a 10-celled coronula (i.e., two tiers of 5 cells each). Plate 82, figs. 3 and 4, indicate the corticationof the normally diplostichous *Chara vulgaris* to be triplostichous; and in fig. 8 the normally triplostichous *Chara fragilis* is illustrated as diplostichous. The figures for this group seem to be rather inaccurate in general, to judge from other published figures for the same species and their types. It is to be hoped that these figures are not a fair sample. Since, however, the author does not apply the type method, one is not surprised to find illustrations and descriptions that are not what might be expected to be attached to a particular name. There is little ostensible display of concern for taxonomic innovation or nomenclatural precision. Such must be the major concern of monographic work and were quite correctly not emphasized among the author's objectives in producing this excellent floristic treatment. If one gave monographic consideration to each entity in such a flora it would be impossible to complete the work. Few authors nowadays have the courage to recognize this

limitation and to produce an honestly floristic treatment devoid of other pretence.

The manuscript has been so long awaiting publication that the author has found it impossible to keep entirely up to date. Thus one finds the incorrect names *Sphaerella* and *Microcystis* instead of the correct names *Haematococcus* and *Polycystis*. Some of the longer-recognized adjustments might have been included, though, such as the replacement among the red algae of the familial name Chantransiaceae, applicable to some green algae, with the more applicable name for the group treated, Acrochaetiaceae.

Original illustrations of most of the over 1000 species have been included. The illustration of such a large number of species was a monumental accomplishment in itself. The detailed presentation of essential measurements and the ecological notes with each description lead to the prediction of a wide and successful use of this book for identification. At first thought it might seem desirable to have included the extralimital ranges of the species treated, but that is done in effect for these freshwater algae by giving their habitats; for the freshwater algae of a given habitat are about the same wherever in the world that habitat is found. Thus throughout the world in brine pools one finds *Dunaliella salina*, in maritime situations on trees and rocks exposed to spray-bearing winds one finds certain species of *Trentepohlia*, and in barnyard pools those certain species of euglenoids.

Certainly this impressive volume, despite its cost, should be on every freshwater phycologist's shelves, and the Cranbrook Institute of Science can be proud of its sponsorship of this publication.

M. DOTY

PUFFBALLS AND THEIR ALLIES IN MICHIGAN. *By Alexander H. Smith. University of Michigan Press, Ann Arbor.* $3.00. xii + 131 pp. + 43 pl. 1951.

In a study of the fleshy Basidiomycetes of Michigan extending over a period of more than 17 years, the author has recognized 83 species and 4 forms that belong to the Gasteromycetes, the name given usually to the fungi known as puffballs and their allies. These represent 8 of the 9 orders which the late Zeller considered valid for the whole world. Of the 32 families and 111 genera recognized by Zeller, 19 families and 30 genera are listed by Smith as occurring in Michigan. Smith suggests that many of the missing families and genera will probably be discovered eventually in Michigan, especially in the northern portion of the state where the ecological conditions are more similar to those in the states of the Pacific Northwest where many of these are known to occur.

The species reported from Michigan vary in size from the minute genera *Gasterella* and *Gasterellopsis*, scarcely over 1 or 2 mm. in diameter, up to the giant puffball *Calvatia gigantea*, which sometimes attains a diameter of over 1 meter. Many of the medium-sized to large species are edible when collected in the right stage of development, and no species is known to be dangerously poisonous.

The 43 plates are from excellent photographs, mostly by the author but a few from a colleague, E. B. Mains. The arrangement of the orders and families follows that of Zeller. The names are in accordance with the International Rules of Botanical Nomenclature. It would have been helpful if synonyms had been given where the present, valid names differ from those used in some of the older works such as Coker and Couch, or Lloyd.

This little book will be very helpful to persons interested in the identification of Gasteromycetes from Michigan and adjacent regions. Its very excellence suggests that it may so stimulate the study of these fungi in Michigan that a new edition may soon be necessary because of the discovery of many species not yet identified with certainty from that state.

ERNST A. BESSEY

A MANUAL OF THE MOSSES OF WESTERN PENNSYLVANIA AND ADJACENT REGIONS. *Second Edition. The American Midland Naturalist, Monograph No. 6. By O. E. Jennings. Edited by John D. Mizelle. University of Notre Dame Press, Notre Dame, Ind.* $4.25. xii + 396 pp.; text ill. 1951.

Nearly a century ago, William Starling Sullivant established a tradition for very high standards for illustrations of American mosses, a tradition that has been too often ignored by his successors. In 1913, however, O. E. Jennings of the Carnegie Museum, Pittsburgh, published privately one of the best illustrated manuals of its time, in which 54 plates of original drawings represented completely and in considerable detail every species available to him in the region. Because of its wide applicability, far beyond the geographic limitation imposed by the title, this book increased in demand to such an extent that it has been out of print for many years. American bryologists have been waiting with especial impatience for the appearance of this long-delayed second edition. The author was far ahead of his time in adopting Hedwig's *Species Muscorum* (1801) as the basis for the nomenclature of the first edition, a decision not accepted formally until the International Botanical Congress of 1930, at Cambridge. Consequently, there has been surprisingly small need for name changes between the two editions, even though 38 years separate them. A half-dozen new combinations are proposed, all but one (a form) at the varietal level. This second edition brings up to date the increase in knowledge of geographic distribution of each species within the region treated, and adds 22 species, for which original—and excellent—drawings are published. The

introductory remarks, covering the special morphology of mosses, a brief account of the region and its habitats, "directions for collecting, preparing, and preserving specimens of mosses," and a very usable key to the genera of mosses, are especially helpful features of this book. The descriptions of genera and species are detailed, precise, and somewhat technical for the beginner, were it not for the excellent plates. It is to be regretted that the author did not include notes on the obvious differential characters of species and genera, from his great personal fund of knowledge and his extensive field experience, an omission undoubtedly dictated by limitations of space. Typographical errors are infrequent, and the reproduction of the plates is excellent. At first glance, some confusion may result from the fact that the generic headings in the text are not only set in the same size and face of type as are the specific ones, but are also numbered in the same manner. These criticisms are very minor, and it is safe to predict that this standard work will attain even greater recognition in its improved and enlarged edition.

WILLIAM C. STEERE

FLORA OF THE LAND OF ISRAEL—*Iconography. Plates 1–50.*

By Naomi Feinbrun and Michael Zohary; drawings by Ruth Koppel; edited by the Palestine Journal of Botany, Jerusalem. Hebrew University, Jerusalem. $3.00 (paper, unbound). 11 pp. + 50 pl. 1951.

As the authors state in the Preface, this loose-leaf volume is the "first step towards an Iconography of the local flora" of Palestine. The work does not pretend to be a descriptive flora, but rather an accurate picture book, and as such it is reasonably successful. Fifty species are illustrated by black-and-white line drawings from living plants, often with enlarged structural details of flower parts in addition to the habit sketches. The quality of the drawings is uneven, however, with some illustrations, such as *Cyclamen persicum* and *Celerach*, recalling the old wood blocks of the herbalists. All of the drawings suffer from heavy lines where the flower structure calls for a lighter touch. But the drawings will certainly aid the beginner in the recognition of Palestinian plant species, which is, after all, the prime object of the work.

The 11 pages of letterpress accompanying the iconography is useful text, but would have been easily improved by a consistent presentation. There are notes on recognition points for closely related irises, distribution remarks, life history notes (e.g., the seeds of *Iris tazetta* are usually dispersed by ants), and economic data, all rather heterogeneously thrown into paragraphs. The general distribution of species is often passed over altogether. For example, *Solanum villosum* is noticed as widespread in Israel, but the global range of this immigrant weed, which about parallels the dispersal of the Hebrew people even to the Sacramento Valley of California, is left unnoticed. No authorities are given for the binomials in the text but they are given in the plate legends. The species selected for treatment include ferns, grasses, and trees, as well as bulbous herbaceous plants, of which Palestine supports so many. The materials are evidently those accessible to the artist for portraiture. It is to be hoped that the second volume will include improved textual matter, and will record the local folk names of the plants (if only in translation), in place of the oddities presented in the first series of sketches. "Eruca-like Diplotaxis" for *Diplotaxis erucoides* or "Damascus Gagea" for *Gagea damascena* are unimaginative names of small advantage over the botanical ones. A prospect for the second volume may amount to a tourist walking abroad in the Palestinian countryside and noting a Testicled Bifora growing beside a Tomentose Pycnocycla, not far from a Crisp Hippomarathrum and a Tortuous Deverra. Then, as he retreats, he steps on an Articulated Anabasis and is pricked by a Corymbose Cardopatium.

There is historic interest, quite apart from popular curiosity of a biblical genesis, in the flora of Israel. Beginning perhaps with the 32-page thesis prepared by Bengt Johan Strand for his major professor, Carl von Linné, and entitled *Flora Palaestina* (1756), and continuing down the years with the works of Hasselquist, Clarke, Sieber, Parrot, Kitto, Bové, and Cosson, climaxed by the *Flora Orientalis* (1867), the 19th century brought rich backgrounds for this, the first iconography of the flora of the Holy Land.

JOSEPH EWAN

PLANT PHYSIOLOGY

PHYSIOLOGY OF FUNGI.

By Lilian E. Hawker; foreword by Professor W. Brown. University of London Press, London. 21s. xvi + 360 pp. + 5 pl.; text ill. 1950.

PHYSIOLOGY OF THE FUNGI.

By Virgil Greene Lilly and Horace L. Barnett. McGrall-Hill Book Co., New York. $7.50. xii + 464 pp.; ill. 1951.

The practically simultaneous appearance of these 2 volumes on fungal physiology reflects the tremendous surge of interest in microbiology within the last decade. Perhaps the main stimuli to this surge have been research on the vitamins, the development of antibiotics, and the origin of biochemical genetics; certainly these topics have played a large part in the formulation of these books. Nevertheless, there are fundamental differences in approach which needed to be pointed out.

Lilly and Barnett have produced a treatise which is frankly biochemical in orientation; in fact, of the first 13 chapters fully 11 are almost entirely biochemistry. Hawker, on the other hand, has concentrated on the

more non-biochemical and purely biological aspects of the fungi. As W. Brown states in the Foreword: "The emphasis in mycology, or to use the wider and rather ill-defined word microbiology, is coming more and more to be physiological and biochemical, and the subject is thus tending to pass from the sphere of the biologist. That micro-organisms should be the happy hunting-ground for material of great human value is all to the good, but it would be regrettable if a tendency to make microbiology an appanage of organic chemistry should go too far. In the last resort, the greatest scientific interest concerned lies in the functioning of the organism as a whole, and fungal morphology, in other words the old-fashioned mycology, studied afresh in the light of new physiological and biochemical knowledge, is still a very live and absorbing subject." Lilian Hawker seems to have adopted this as her philosophy. Her book is therefore centered about the functioning organism, with biochemistry merely one aspect of the total picture. Lilly and Barnett, on the other hand, have described what is, in part at least, comparative biochemistry with specific reference to the micro-organism.

Hawker starts with a discussion of the life cycles of fungi, then passes to such topics as their growth and variation, nutrition, respiration, sporulation, germination and survival of spores, and interactions with other organisms. Lilly and Barnett organize their early discussions about such topics as culture media, growth, enzymes, essential elements; carbon sources, hydrogen-ion concentration, vitamins and growth factors, fungi as assay organisms, metabolic antagonists, the action of fungicides, and metabolic products. Their last 5 chapters deal with the more physiological topics, such as sporulation, spore germination, the physiology of parasitism, and the inheritance and variation of physiological characters.

Both volumes seem to be competent assessments of the subjects of interest to their authors. Of the two, Hawker's Physiology of Fungi is probably the more succinct and better organized. However, in this age of biochemistry, the book of Lilly and Barnett will undoubtedly find the wider use.

ARTHUR W. GALSTON

NITROGEN IN THE LIFE OF PLANTS.

By Dmitrii N. Prianishnikov; translated from the Russian by S. A. Wilde. Kramer Business Service, Madison. $2.75 (paper). ii + 109 pp.; ill. 1951. This book was published by Prianishnikov three years before his death in 1948. It contains the views and results of a man who worked for more than 50 years in the field of plant metabolism. In addition to the work of Prianishnikov and his students, the book also reviews and summarizes the results of other investigators, primarily European. Most of the textbooks of plant physiology now in use in this country do not mention his work. This is not because it was unimportant but mainly because of the inaccessibility of many of his publications. The present translation will go far to correct this situation.

Aside from its scientific merit, this volume is also a readable account of the personal achievements of a pioneer investigation in plant physiology. Along with Chibnall's *Protein Metabolism in the Plant*, this book might well serve as a syllabus for the "case-history" approach to the teaching of a very important phase of plant physiology.

The book is mimeographed and relatively free of errors. The errors noted were mainly in the structural formulae of the various carbohydrate intermediates. In this day of expensive books, it is a pleasure to find so worthwhile a volume that does not strain the modest book budget of most of us.

G. R. NOGGLE

ECONOMIC BOTANY

THE MOLDS AND MAN. *An Introduction to the Fungi. By Clyde M. Christensen. University of Minnesota Press, Minneapolis; Geoffrey Cumberlege, Oxford University Press, London.* $4.00. viii + 244 pp. 1951. Relatively few attempts have been made to assess and interpret for the layman in non-technical language the role of fungi in relation to human welfare. Drawing widely from the fields of plant pathology, medical mycology, and industrial mycology, Christensen has marshalled a series of examples illustrating the activities of fungi which are both beneficial and harmful to mankind. The partnerships of fungi with other plants, as in lichens and mycorrhizae, and with animals, exemplified by fungus-growing ants, are discussed. Synoptic accounts of flax wilt, late blight of potatoes, the rusts of coffee, white pine, and wheat, the cereal smuts, and heart rot of forest trees cannot fail to impress the reader with the destructive activities of plant parasitic fungi. Human diseases of fungus origin such as ringworm, athlete's foot, and coccidioidomycosis are shown not to be unique, but to have many similarities with fungus diseases of nematodes, insects, fish, and birds. The destruction of commercial products by fungi is treated in a chapter devoted to molds which destroy stored grain, flour, dairy products, timber, fabrics and leather. Man's exploitation of fungi for industrial uses includes the cultivation of mushrooms, the manufacture of cheese, and the technology of securing enzymes, industrial chemicals and drugs from molds. The last chapter is a classification of fungi, in which the author follows the system proposed by G. W. Martin.

F. T. WOLF

AMERICAN WOODS.

By Shelley E. Schoonover. Watling & Co., Santa Monica. $7.50. ix + 250 pp. + 82 pl.; text ill. 1951.

The popularity of woods as a medium for creative design at home has gained enormously in late years, largely through the availability of machine tools of reasonable price, and because of the trend towards functional furniture of simple lines. These tools assure even the amateur craftsman of some measure of success in woodworking, and it was inevitable that a need would arise for more information about our native American woods. S. E. Schoonover, a retired member of the U. S. Forest Service, has now provided this in detail. After an introductory section on tree growth and wood characteristics in terms of cutting, seasoning, grains, and figures, the author has considered some 150 American species from the point of view of their natural appearance, common names in various areas and in the trade, growth range, workability, and usage. A number of colored plates illustrate the various grains and figures which are commonly employed in wood design. The language is non-technical, and a list of references and dealers in woods concludes the book. All in all, it is a most useful volume for the designer and craftsman who may wish to take advantage of the many excellent woods available in this country.

C. P. SWANSON

GENERAL AND SYSTEMATIC ZOOLOGY

COLLEGE ZOOLOGY. *Sixth Edition.*

By Robert W. Hegner and Karl A. Stiles. Macmillan Co., New York. $6.00. xii + 911 pp. + 1 pl. 1951.

This well known college textbook needs no introduction to American teachers. In its latest revision, more than one-half of the illustrations have been redone or replaced, and the glossary has been much expanded. As before, a phylogenetic treatment of the animal phyla has been adhered to, with the more general topics serving either as introduction or as epilogue. For a survey of the animal kingdom, the text is excellent; for a modern approach to biology in general, and to zoology, in particular, it is quite inadequate in those basic subjects of physiology, genetics, and ecology which provide the unifying principles upon which the whole science is founded.

C. P. SWANSON

THE OONOPIDAE OF PANAMA. *Bull. Mus. comp. Zool., Harvard College, Vol. 106, No. 5.*

By Arthur M. Chickering. Museum of Comparative Zoology, Harvard College, Cambridge, Mass. 80 cents (paper). Pp. 207–245; ill. 1951.

No less than 13 new species of spiders, belonging to 7 of the 9 genera in the family, are described in this brief paper.

CATALOG OF THE TERMITES (ISOPTERA) OF THE WORLD. *Smithsoniam Misc. Coll., Vol. 112. Publ. 3953.*

By Thomas E. Snyder. The Smithsonian Institution, Washington, D. C. Paper. 490 pp. 1949.

The preparation of a complete catalog of the termites of the world is a truly monumental work. It includes the fossil termites as well as the living species, is well indexed, and includes an extensive bibliography.

THE PHYLLOPHAGA OF HISPANIOLA (COLEOPTERA: SCARABAEIDAE). *Bull. Mus. comp. Zool., Vol. 106, No. 5.*

By Milton W. Sanderson. Museum of Comparative Zoology, Harvard College, Cambridge, Mass. $1.00 (paper). Pp. 249–283 + 6 pl. 1951.

Fifteen new species of the beetle *Phyllophaga* are added here to the 10 previously known from Hispaniola.

LIST OF DANISH VERTEBRATES. *Fishes, Amphibians and Reptiles, Birds, Mammals.*

By Anton Fr. Bruun, J. R. Pfaff, Bernt Løppenthin, and Magnus Degerbøl. Dansk Videnskabs Forlag (Danish Science Press), Copenhagen. Kr. 10.50 (paper). 180 pp. + 1 map. 1950.

This list is preceded by a short introduction which summarizes the occurrence not only of the living species but also of those recently extinct; and the list is followed by an adequate index.

The list itself includes 183 marine fishes, 32 freshwater or brackish-water fishes, 3 species of salamanders and 11 of anurans, 3 species of lizards and 3 of snakes, an extinct tortoise, 343 species of birds, 42 land mammals, and 20 marine mammals.

ECONOMIC ZOOLOGY

SUCCESSFUL POULTRY MANAGEMENT. *2nd Edition.*

By Morley A. Jull. McGraw-Hill Book Co., New York, Toronto, and London. $5.00. xii + 447 pp. + 1 folding chart; text ill. 1951.

This book follows somewhat the same course as the author's *Poultry Husbandry*, but is concerned more with how to do things than with the reasons for doing them. It is intended for people who are raising poultry or would like to do so. Its 12 chapters deal with such things as keeping good stock, culling, breeding, rearing, housing, feeding, controlling disease, marketing and, finally,

how to combine efficient conduct of all these operations so successfully that the poultryman can pay not only his feed bill, but also his grocery bill, and perhaps have a little left for Mr. Truman.

The book is evidently intended also for students of agriculture, for at the end of each chapter there is a useful list of Supplementary Activities which for many a teacher will prove to be an ever-present help in time of trouble. These lists include not only problems of various kinds, but also demonstrations and other activities in which a whole class may engage to ensure that practical touch which is usually more attainable in the hen house than in the classroom. During the past decade, the widespread use of automatic machinery for feeding and watering hens, for grading eggs, and for many other operations on the poultry farm has brought to many a harried poultryman the problem of what to do with all the idle hours that efficiency has thus forced upon him. The reviewer suggests that he might well spend some of them in reading this book.

In its useful appendix, he will find a list of 59 agricultural colleges in the United States and Canada to which he can write for bulletins if he has the time, the will, and the crust to do so. (Jull thoughtfully suggests that each poultryman concentrate on the institution of his own state.) There is also a list of 54 publications about poultry available from the U. S. Department of Agriculture, another of pertinent films (with sources), and a nice list of 23 useful books. Considering all these opportunities, no idle poultryman should get into mischief while the water bubbles merrily away in his drinking fountains.

F. B. HUTT

INTRODUCTORY ANIMAL HUSBANDRY. *Revised Edition.* *By Arthur L. Anderson. Macmillan Co., New York.* $6.00. x + 701 pp.; ill. 1951.

This book is written primarily for the beginning college student to acquaint him with the fundamental problems of livestock production in the United States. The same basic pattern of presentation of subject matter is followed for each type of livestock: beef cattle, dairy and dual purpose cattle, swine, sheep, horses and mules. The information on each of these includes the general view of the industry; types, market classes, and breeds; meat processing; and feeding, breeding, and management. The book, previously published in 1943, has been brought completely up to date. It is well illustrated with more than 300 pictures, charts, and graphs.

FREDERICK N. ANDREWS

DAIRY SCIENCE—*Its Principles and Practice. Second Edition.*

By W. E. Petersen; edited by R. W. Gregory. J. B. Lippincott Co., Chicago, Philadelphia, and New York. $5.50. viii + 695 pp.; ill. 1950.

This book covers the entire field of dairy husbandry. It summarizes the pertinent information on such diverse subjects as dairying in ancient Mesopotamia, the economics of the cheese industry, basic Mendelian inheritance, the value and handling of barnyard manure, and the physiology of milk secretion. Eight chapters on the economics of milk production and one on microbiology were contributed by H. C. Trelogan of the U. S. Department of Agriculture, and by E. O. Herreid of the University of Illinois, respectively.

The author is careful to point out that because of the wide range of subject matter controversial matters and current researches can be mentioned only in passing, if at all. For the more critical college student of dairy production a list of supplementary reading for each chapter is included in the appendix. The treatment of the nutritional requirements of dairy cattle in a chapter of 25 pages, of the fundamental considerations of heredity in 8 pages, and of the physical and chemical properties of milk in 7 pages will hardly satisfy the specialists in these fields. Yet Petersen, who is an international authority on the physiology and biochemistry of milk secretion, has allowed himself only 11 pages for the physiology of the mammary system. This degree of brevity disqualifies this book as a reference work for the more advanced student, but makes it well adapted for the undergraduate student for whom it was written and for the practical dairyman and vocational agricultural student.

The book is written in an easy readable style and contains a great number of tables, graphs, drawings, and photographs. Most of the illustrations are clear and self-explanatory; a few dealing with cellular structures are disappointing to the author and reader alike.

FREDERICK N. ANDREWS

HORSE HUSBANDRY.

By M. E. Ensminger. Interstate, Danville, Illinois. $3.00. 336 pp.; ill. 1951.

The author has, in a day when the horse appears to be nearly completely displaced as a source of motive power, written a completely modern textbook dealing with all phases of horse production. The subjects dealt with range from the evolutionary development of the horse to the basic principles of equitation, including the proper dress of the equestrian. The types, classes, and breeds of light and draft horses are briefly but adequately described. The breeding, feeding, and general management of various types of horses are discussed. An excellent chapter on the diseases and parasites of horses and mules, with Leo Bustad as coauthor, is included. The book should serve the needs of secondary

and college students and all others interested in horse husbandry.

FREDERICK N. ANDREWS

PRACTICE OF WILDLIFE CONSERVATION.

By Leonard W. Wing. John Wiley & Sons, New York; Chapman & Hall, London. $5.50. xii + 412 pp.; ill. 1951.

The relatively new technical field of wildlife management has by now its own thousands of publications, plus those of bordering fields. Wing has undertaken to extract essential facts from this literature and to present them in an understandable manner. The scope of his book ranges from fundamental biology through brief accounts of species classified according to habitats to different aspects of management. Both terrestrial and aquatic animals, non-game as well as game, are discussed.

The treatment of specific topics is often sketchy, and most veteran professionals in the field are practically sure to be dissatisfied with the way in which their speciality is handled. This may be largely unavoidable because of the problems inherent in condensations, but the book does have many recognizable loose ends and errors of fact, flat assertions on subjects that are at least debatable, and examples that are hardly typical of what they are intended to illustrate, though they may themselves be the product of reputable investigations.

Practice of Wildlife Conservation, with its generally (but not invariably) readable style and elementary content, is more suitable as a textbook for undergraduate or perhaps high school courses (or as a source of perspective for game wardens, sportsmen, legislators, and the interested lay public) than for advanced students. I would rate the concluding chapters on legal status and the administration of wildlife as among the most informative.

PAUL L. ERRINGTON

THE POTATO MOTH, GNORIMOSCHEMA OPERCULELLA (ZELL.) AND ITS CONTROL IN AUSTRALIA. *Bull. 248.*

By G. A. H. Helson. Commonwealth Scientific and Industrial Research Organization, Melbourne, Australia. Free upon request (paper). 27 pp. 1949.

DECLINE OF THE LAKE TROUT FISHERY IN LAKE MICHIGAN. *Fishery Bull. 60. Fishery Bull. Fish & Wildlife Service, Vol. 52.*

By Ralph Hile, Paul H. Eschmeyer, and George F. Lunger. United States Department of the Interior, Fish and Wildlife Service, Washington, D. C. 20 cents (paper). Pp. 77–95. 1951.

BEAVER MANAGEMENT AND ECOLOGY IN WYOMING. *Federal Aid in Wildlife Restoration Project, Wyoming 31-D and 30-R. Bull. No. 6.*

By James E. Grasse and Euvern F. Putnam. Wyoming Game and Fish Commission, Cheyenne. 25 cents (paper). viii + 52 pp.; ill. 1950.

ANIMAL MORPHOLOGY

THE ANATOMY OF MAN AND OTHER ANIMALS, *or Brothers Under the Skin.*

By D. Stark Murray and Grace M. Jeffree; colour plates by E. C. Mansell. Watts & Co., London. 18s. x + 158 pp. + 20 pl.; text ill. 1950.

It is uncertain to what group this book is addressed, the preface simply stating the hope that further study will be stimulated. It should certainly accomplish this with the casual lay reader because of the fascinating way in which the subject matter is handled. The biologically trained reader, however, will find it so replete with categorical error that the reverse may well occur.

The first 8 chapters are general, ranging all the way from the evolutionary divergence of plants and animals to locomotion. The remaining 7 chapters deal with organ systems, the comparative anatomies of which are traced through their evolutionary vicissitudes. There are numerous line drawings in black and white, a number of which are embellished with parts in red, and there are 4 plates in full color. The latter are the prettiest I have ever seen. Yet one is bound to wonder what sort of paleontological revelation could have informed the artist that the archaeopteryx posessed blue, green, and gold wings, a white body, and a green tail. After all, the poor slighted *Ramphorhyncus* (spelled wrong, but still a pterodactyl) is only dirty yellow all over! More fetching is the bright green *Amoeba*.

The authors have a genuine gift for generalization, but its effectiveness is marred by frequent untenable statement of detail. For example, the mouth armatures of marsupials are contrasted as a group to those of other mammals, a good point, but these animals are stated to be "confined to the Australasian continent." The prevalence of such errors detracts from the value of an otherwise remarkably interesting book. It is indeed a Gargantuan bite of biology, somewhere between the technical and the popular, but one that cannot be recommended on account of the reasons stated above.

F. N. LOW

A SYNOPSIS OF SURGICAL ANATOMY. *7th Edition.*

By Alexander Lee McGregor; foreword by Harold J. Stiles. Williams & Wilkins Co., Baltimore (printed in Great Britain). $6.50. xii + 778 pp.; ill. 1950.

This formidable volume has passed through 7 editions in less than 20 years and is, to all appearances, still

growing. The present edition has some 70 new illustrations, with new chapters on trans-thoracic surgery and the surgery of the blood vessels. Other sections have been altered and brought up to date.

The first part, of 339 pages, deals with normal anatomy. It restricts itself to anatomical description with some physiological function. The second part, of 396 pages, deals with abnormal anatomy. A long section covers the anatomy of congenital errors and is mainly descriptive, with consideration of pathological consequences. The remaining portions deal with surgical procedures of various sorts. The illustrations are simple line drawings.

The tone of the whole book is simple, clear, and authoritative. The author, a surgeon in Johannesburg, S. Africa, seems to project that quiet scholarly competence which is somehow a characteristic product of the British schools. The reader must certainly be safe in his hands.

F. N. Low

FUNCTIONAL NEURO-ANATOMY, *Including an Atlas of the Brain Stem. 2nd Edition, thoroughly revised.*
By A. R. Buchanan. Lea & Febiger, Philadelphia. $7.50. 323 pp.; ill. 1951.

The main body of this work is essentially unchanged, but an atlas has been added and the whole volume is printed on better quality paper. The review of the first edition (*Q.R.B.*, 24: 65, 1949) covers the first 225 pages of this one, since pagination and plates are quite unchanged. An occasional new paragraph has been added without other alteration of the original text.

The new atlas consists of 37 plates of cross sections extending from the pyramidal decussation to the rostrum of the corpus callosum. The left half of each of these plates is photographic, while the right half is a simple line drawing with major structures labeled. The facing page contains a brief description of the level pictured and a separately numbered key plate (the same for every level) showing the direction of the cut. The appearance is neat. A 4-page index at the end indicates the pages in the atlas where listed structures are illustrated.

Additions have been made to the bibliography. This textbook remains a routine presentation of its subject, commendably short but rather undistinguished.

F. N. Low

ANIMAL PHYSIOLOGY

CORONARY CIRCULATION IN HEALTH AND DISEASE.
By Donald E. Gregg; foreword by Carl J. Wiggers. Lea & Febiger, Philadelphia. $4.50. 227 pp.; ill. 1950.

A concise, analytical monograph of great importance. The study of coronary physiology is fundamental to an understanding of coronary disease, perhaps the most critical present medical problem. The author has been actively associated with the field for 15 years by virtue of his own research. His book is not a compendium of results and theories but a mature orientation of data where conclusions do not have equal value, and where results are appraised in relationship to the adequacy of the experimental method. The author's own work, on which the volume draws freely, is based largely on the study of the normally beating dog's heart in situ, and represents a more integrated approach than is commonly pursued.

The statistical problem of coronary artery disease is briefly presented. The next chapter, one on anatomy, is unusually stimulating by virtue of its brevity and completeness. Experimental apparatus and the techniques necessary for the study of mean and phasic pressures, coronary flow, and the metabolism and work of the heart are clearly outlined, with the necessary discussion especially as to their adequacy. The results obtained for coronary flow in the dog and in man by various methods, together with the determinants of coronary flow and the influence of drugs, are recorded in detail. An excellent section is included on work and metabolism. The final chapter discusses coronary circulation in heart disease with special reference to coronary atherosclerosis. This is a lucid presentation outlining current knowledge and the lack of any satisfactory therapy, and pointing out the need for suitable experimental preparations. In this respect it will be a surprise to many to find that no standardized chronic heart failure preparation is now available. The entire monograph is fully annotated, 198 references being included for the last chapter alone.

No volume of similar intent or scope is available. Gregg is to be congratulated on a work that will be widely used both for reference and study.

E. Converse Peirce, 2nd

BRAIN METABOLISM AND CEREBRAL DISORDERS.
By Harold E. Himwich. The Williams & Wilkins Co., Baltimore. $6.00. xii + 451 pp.; ill. 1951.

There has long been need for a textbook that would comprehensively review the subject of brain metabolism in its various aspects. Although there have been some attempts in the past to deal with the biochemistry of the brain, the results were textbooks of biochemistry with only incidental references to its application to the brain.

H. E. Himwich, one of the foremost students of cerebral metabolism, has now filled this need, and with this book has made a truly outstanding contribution. It should please the serious student of the subject, the

clinician concerned only with the medical aspects, the practitioner or medical student desiring to broaden his knowledge, and the general biologist or physiologist requiring a reference source. In part, Himwich accomplished this by the judicious use of footnotes which contain detailed information that may be required by the serious student, yet which can be ignored by other readers without impairing the readability and continuity of the text. Almost 1100 references are critically evaluated as objectively as it is possible for an investigator to do, particularly one who has lived with the general subject for over a quarter of a century.

Himwich will probably be taken to task on some of his interpretations by a few workers in the field, especially when he deals with the foodstuffs that the brain can oxidize, or his application of some data as additional evidence for Hughling Jackson's hypothesis of the functional organization of the central nervous system. This, of course, is unavoidable. One tries to be objective; as Himwich puts it, "one can only see through our own eyes."

The book is divided into two parts: I, The Energetics; II, Patterns of Nervous Activity. The chapters dealing with the former are exceptionally thorough and readable. The chapters on therapeutics and their application to brain metabolism, as well as Part II, should be of especial interest to the clinician.

The book is written in conversational style, is exceptionally well indexed both as to subject and author, and is unhesitatingly recommended as a valuable addition to the personal libraries of all students of biology and medicine.

DAVID B. TYLER

ANTIHISTAMINE AGENTS IN ALLERGY. *Ann. N. Y. Acad. Sci., Vol. 50, Art. 9.*

By Frederick F. Yonkman and 15 other authors. The New York Academy of Sciences, New York. $3.00 (paper). Pp. 1013–1208; ill. 1950.

This important conference covered the occurrence and action of histamine and other metabolites in anaphylactic shock and allergy, as well as the pharmacology, specificity, and mode of action of the antihistamine drugs. The contributors included Sir Henry Dale; Bradford N. Craver; Carl A. Dragstedt; M. Rocha e Silva; E. T. Waters; Norbert Fell; Daniel Bovet; R. L. Mayer; Earl R. Loew; Rolf Meier, Charles F. Code, John U. Keating, and Milo D. Leavitt, Jr.; Samuel M. Feinberg; J. A. Wells; and Bret Ratner. Most of the papers are followed by discussion, and there is additional general discussion in two sections at the end. Indispensable as it will be to those interested in these fields, the publication would have been made considerably more useful had an index been prepared.

YOUR BODY AND HOW IT WORKS.

By F. R. Elwell. Cambridge University Press, New York & London. 80 cents. vi + 111 pp. + 2 pl.; text ill. 1950.

This very elementary and exceedingly brief book for the British 13- or 14-year-old student may be of interest to American teachers at the corresponding level of the secondary school.

ANIMAL NUTRITION

THE VITAMIN B COMPLEX.

By F. A. Robinson. John Wiley & Sons, New York. $9.00. xii + 388 pp. 1951.

This book is a critical review of the vitamin B complex. The plan in the discussion of each vitamin follows the order: historical account, isolation, chemical constitution, synthesis, properties, stability, biological estimation, microbiological assay, chemical estimation, occurrence, effect of deficiency (a) in animals, and (b) in man, effect of excessive dosage, metabolism, intestinal synthesis, animal and human requirements, pharmacological action, function, role in the nutrition of microorganisms, effect on higher plants, requirement of insects, and analogues.

Following this plan the author discusses aneurine (thiamine), riboflavin, nicotinic acid (niacin), pyridoxine, pantothenic acid, biotin, the folic acid complex, vitamin B_{12}, p-aminobenzoic acid, inositol, choline, and miscellaneous water-soluble growth factors. In the latter category he includes vitamins B_3, B_4, B_8, B_{10}, B_{11}, B_{13}, B_{14}, vitamin L, factors U, W, R, and S, and miscellaneous growth factors for animals and for microorganisms.

The author states that in the preparation of this book he examined all the published literature relating to the subject and selected and arranged the most important facts. This monumental task he has accomplished with marked success, and in doing so he has produced a valuable reference volume which will be welcomed by all investigators and teachers, as a reliable source of information and interpretation.

E. V. MCCOLLUM

HEALTH THROUGH NUTRITION.

By Lelord Kordel. World Publishing Co., Cleveland and New York. $3.00. 315 pp. 1950.

This volume is made up of such a weird concoction of science, pseudo-science, and dietary fads that it will be most difficult for the average reader to sift the authentic information from the unauthenticated claims, and to remain unaffected by the latter. Although there is a full-page warning (in the back of the volume) that the author is not a physician, and that he is not attempting to

diagnose ailments or prescribe treatment, and further, that it is dangerous for the average person to diagnose his own ailments and prescribe for them, the subject is presented in such a way that the reader is likely to interpret them in a manner directly opposed to those stated precautions. In the face of such glowing accounts as those of the use of glutamic acid and thiamin for improvement of the intellect; of fenugreek seeds for "sludged blood"; of unsulphured apricots for anemia; of vitamins E for heart trouble; of the author's "purifying diet" (p. 136) for all sorts of gastro-intestinal ailments; of the herb "eyebright" for eye difficulties; and of cucumber juice "coctails" for arthritis, it will be most difficult for the faddist to refrain from trying some of these remedies for his own ailments.

There is nothing here that will interest the serious student of nutrition, unless, of course, he is interested in curiosa.

B. AUBREY SCHNEIDER

CLINICAL NUTRITION.

Edited by Norman Jolliffe, F. F. Tisdall, and Paul R. Cannon. Paul B. Hoeber, New York. $12.00. xvi + 926 pp.; ill. 1950.

This handbook will have wide appeal. It is prepared by 36 well-known students of the various subjects covered and undoubtedly will serve as a major text in the field of nutritional abnormalities.

The first part is concerned with the diagnosis of nutritional deficiencies. The frank nutritional deficiencies are easily recognized, but in this country are not a major problem since they occur so infrequently. The real difficulty lies in detecting the less severe degrees of malnutrition, and it is these lesser signs that are so frequently overlooked. Without in the least detracting from the excellence of the other 5 chapters of Part I, one can say that Chapter 3, Clinical Signs, prepared by Jolliffe, Tisdall, and Cannon, will be of especial interest to the practicing physician. The use of a number of plates in full color adds greatly to the value of the chapter.

The second part of the text is divided into 24 chapters, each of which is concerned with malnutrition of specific individual nutrient elements.

Part III deals with therapy and prevention. Considerable attention is paid to specific diet plans for the various clinical problems covered in the first two parts. There is also an extensive section on obesity, and the performance of individuals in various occupations as affected by their nutritional status.

This book is unhesitatingly recommended as an invaluable addition to the personal library of the practicing physician, medical teacher, and medical student.

DAVID B. TYLER

NUTRITION AND ALCOHOLISM.

By Roger J. Williams. University of Oklahoma Press, Norman. $2.00. x + 82 pp. 1951.

This is a popular presentation of the confused and complicated subject of alcoholism. R. J. Williams, director of the Biochemical Institute of the University of Texas, here sponsors the theory that alcoholism is a physiological problem caused primarily by malnutrition. In developing this theme it is indicated that individual variability, manifested in so many familiar ways, is to be found also in individual requirements for certain food elements. Alcoholics are believed to have abnormally high nutritional requirements, and if these are not met, deficiencies result and a craving for alcohol develops. The treatment suggested for alcoholism is by nutritional supplementation. The author also states: "there is the additional possibility that by similar nutritional means—using the same principle—various obscure diseases, even mental troubles, can be benefited." Written primarily for the layman, neither experimental data nor a critical appraisal of research findings is presented.

R. VAN REEN

BIOCHEMISTRY

PHOSPHORUS METABOLISM. *Volume I. A Symposium on the Role of Phosphorus in the Metabolism of Plants and Animals. Sponsored by the McCollum-Pratt Institute of the Johns Hopkins University.*

Edited by William D. McElroy and Bentley Glass. The Johns Hopkins Press, Baltimore. $10.00. 762 pp.; ill. 1951.

This book, the reviewer believes, is destined to become an historical document, and will provide a rich reference source for future historians of biochemistry. Every biochemist, particularly if his primary interests lie in the dynamic rather than the more static aspects of the subject, will feel indebted to the organizers of this symposium, and the more so because the deliberations of the contributors have appeared in book form at such an unusually early date. It is excellently produced (the reviewer detected very few typographical or other errors) and is comfortable to read, an important feature in a book such as this, which must be read by every biochemist who wishes to keep abreast of his subject.

The material covered is divided into eleven sections bearing the following titles:

I. Metabolism of Polysaccharides and Disaccharides.
II. The Metabolism of Hexose Phosphates.
III. The Metabolism of Pentose and Triose Phosphates.
IV. Recent Investigations on the Formation and Utilization of Active Acetate.

V. Oxidative Phosphorylation during Electron Transport.
VI. The Metabolism of Phosphorus-containing Coenzymes.
VII. The Biochemistry of Inorganic Pyrophosphates and Metaphosphates.
VIII. The Influence of Inorganic Ions on Phosphorylation Reactions.
IX. The Chemistry and Thermodynamics of Phosphate Bonds.
X. The Utilization of Phosphate Bond Energy in Biological Systems.
Summary.

The discussions provoked by each of these groups of communications are fully reported and add much to the value of the book, for they serve not only to clarify a few obscurities in the communications themselves, but also to give occasional glimpses into the probable future.

In general the contributions are clearly and critically written, and speculation is kept in its proper place and proportion—always an important feature in such a book as this, which is destined to be read by many whose interest in phosphorus metabolism is great but whose first-hand knowledge of the field is comparatively small. The reviewer was particularly happy to find in the bibliographies many more references to work done outside the American Schools than is usual in American publications of this kind; the contributors have not in general hesitated to acknowledge the work of biochemists abroad.

To choose particular contributions for particular mention would perhaps be invidious, but the concluding summary by Bentley Glass stands out as a masterly review which places in its proper perspective nearly every topic touched upon by the contributors. Just as a preface is the part of a book that is written last and placed first, Bentley Glass's summary, which is placed last, should be read first, "to show in little, by what Materials, with what charge, and by how many Hands, that (which) is afterwards to be rais'd," as Thomas Spratt wrote of his *History of the Royal Society*.

The use of a large number of abbreviations, some of which are not yet familiar to biochemists in general (e.g. AMC, ASF, FGAP, PFK) and have not yet found any very wide usage (in contrast to ATP, DPN, TPN), is to be deprecated. They save little ink, paper, or space, and the reviewer found the necessity of referring continually to the printed list of abbreviations irritating in the extreme, and often disruptive to his train of thought. But even so, few more useful contributions to the general literature of biochemistry have ever appeared. This admirable publication deserves and will assuredly find a vast public among the biochemists of the world, and do much to stimulate fresh interest and research in this largest of all fields of modern biochemistry.

ERNEST BALDWIN

ORGANIC SYNTHESES. *An Annual Publication of Satisfactory Methods for the Preparation of Organic Chemicals. Vol. 31.*

Edited by R. S. Schreiber and others. John Wiley and Sons, New York; Chapman & Hall, London. $2.75. vi + 122 pp.; text ill. 1951.

This volume contains the syntheses of 41 organic chemicals and an index to both this volume and the preceding one. The synthesis of ethyl pyruvate is likely to be particularly interesting to biochemists.

LABORATORY MANUAL OF BIOCHEMISTRY. *Third Edition.*

By Benjamin Harrow, Gilbert C. H. Stone, Harry Wagreich, Ernest Borek, and Abraham Mazur. W. B. Saunders Company, Philadelphia and London. $2.25 (paper). x + 149 pp.; ill. 1950.

This excellent manual has been considerably revised. It is exceptionally well indexed, contains a useful appendix, and is adequately illustrated. It can be recommended for use for either an elementary introductory course in biochemistry or for a course that covers two semesters of laboratory work.

DAVID B. TYLER

THE SULPHONAMIDES.

By F. Hawking and J. Stewart Lawrence. H. K. Lewis & Co., London. 42s. viii + 389 pp. + 12 plates; text ill. 1950.

This is a very comprehensive review of the literature dealing with sulphonamides (over 1,000 references in the bibliography), with particular attention paid to the chemical nature, mode of action, pharmacological properties, and clinical application of these drugs. The book is well organized, well written, and well illustrated, but the indexing is somewhat inadequate. The volume should be a valuable addition to the library of the clinician and pharmacologist concerned with problems in the field of chemotherapy.

DAVID B. TYLER

ANTIPYRINE. *A Critical Bibliographic Review. Monographs of the Institute for the Study of Analgesic and Sedative Drugs, III.*

By Leon A. Greenberg; introduction by Howard W. Haggard. Hillhouse Press, New Haven. xvi + 135 pp. 1950.

This monograph summarizes in 57 pages of text 1735 papers dealing with antipyrine, with particular reference to its physico-chemical properties, fate in the body, pharmacology and toxicology, therapeutic uses, poisoning, tolerance, addiction, and habituation. The book

should be of interest to the more serious students in this field.

DAVID B. TYLER

IMMUNO-CATALYSIS AND RELATED FIELDS OF BACTERIOLOGY AND BIOCHEMISTRY. *Second Edition, Revised and Enlarged.*

By M. G. Sevag; preface by Stuart Mudd. Charles C Thomas, Springfield, Ill. xx + 547 pp. 1951.

Six years after the first edition of this book a second is published. Its volume has increased from 232 to 547 pages, 100 of these containing a long list of 1060 references and an author as well as subject index. The book contains more than the title indicates. The author discusses critically not only immunological problems but also many other topics such as the action of enzymes, mechanism of clotting, and hemolysis. Sevag defines "an enzyme (or an antigen) as any protein capable of performing a specialized physiological function in accordance with the well known criteria of ideal catalysis." Hence the role of the antigen in antibody formation is considered to be that of a catalyst. No doubt, there is enzymatic action involved in antibody formation; but is the antigen the catalyst? Although the reviewer still does not know the answer to this question, he recommends the book as a rich source of information and as very stimulating reading to all those interested in immunological phenomena.

FELIX HAUROWITZ

HEALTH AND DISEASE

VIRUS AND RICKETTSIAL DISEASES.

By S. P. Bedson, A. W. Downie, F. O. MacCallum, and C. H. Stuart-Harris. Williams & Wilkins Co., Baltimore. viii + 383 pp.; ill. 1950.

This book was written for the purpose of recording concisely current knowledge of virus and rickettsial diseases and was prompted by the fact that advances have been rapid during the last 15 years. It is directed to the practicing physician whose knowledge, it is pointed out, through no lack of his interest, may lag far behind current reports from the field of virus research.

This work is written by 4 British scientists who have had long experience in research on viruses and have made valuable contributions in that field. As indicated in the Preface, the space devoted to a given virus depends more on what is known about it than upon the prevalence or seriousness of the disease which it causes. For instance, some 8 pages are devoted to the virus of herpes simplex and the infections which it causes, while less than 3 pages are used to discuss rubella, 5 for measles, and 3½ for infectious mononucleosis.

After 4 introductory chapters treating respectively general considerations regarding viruses, immunity, the natural history of virus disease, and chemotherapy, the rickettsial and viral diseases of man are taken up individually or by logical groups. Practically all the well established viral diseases are included, with the exception of a few that have been described by American workers but have not yet been encountered in Great Britain. Viral diseases that are primarily veterinary problems are not discussed, with the exception of 3 that occasionally produce minor human infection. One chapter on the viruses of bacteria (bacteriophage) is included because of the importance of the information regarding host-virus relationships that has been provided by investigations on bacteriophages.

Although achieving the goal of brevity and conciseness in this work, the authors have not failed at the same time to accomplish a surprising degree of thoroughness and to provide much detailed information. Although the bulk of the discussion in a given chapter is on the virus itself, concise information is included on clinical and other aspects of the disease or infection produced. Epidemiology and the various diagnostic aids that the laboratory can supply are stressed. The chapters are divided into sections, labelled in bold-faced type, allowing rapid scanning for specific information. A brief description of the discussion on psittacosis will illustrate the presentation on the various diseases. After an introductory paragraph giving the main points in the history of this disease and appropriate information on its geographical distribution and prevalence, the following sections appear: clinical picture, etiology, characters of the virus, laboratory diagnosis, epidemiology, control, and treatment.

There is a 3-page appendix consisting of a valuable tabulation of essential information for the physician, indicating the type of laboratory tests used for diagnosis in each of the diseases, e.g., virus isolation or appearance of antibody in serum, the specimens that should be taken during the acute and convalescent stages, and an estimation of the time required before preliminary and final results will be available. The index appears to be adequate, and at the end of each chapter there is a list of appropriate references including both older and current titles. The work is illustrated with 33 half-tone engravings which in most cases are excellently reproduced. The entire book is printed on a suitable paper. The work will be of value not only to the physician or medical student but to all students of infectious disease.

F. B. GORDON

AN INTRODUCTION TO PATHOLOGY.

By G. Payling Wright. Longmans, Green & Co., New York (printed in Great Britain). $6.00. x + 569 pp.; ill. 1950.

This interesting volume should prove to be a valuable

adjunct to the study and understanding of general pathology. It stresses the experimental approach, describing physiological as well as anatomical changes in disease. This is a radical departure from the purely anatomical approach to pathology utilized in most recent American textbooks, where experimental evidence for the opinions expressed is often completely lacking.

Unfortunately, this book cannot replace a standard pathology textbook because its scope is too narrow. Although over 500 pages in length, the author covers a limited number of subjects. He is interested in the relation of genetics to disease; in certain aspects of infection such as bacterial invasion, bacteriostasis, and inflammation; in some tissue reactions and degenerations; and in the effects of circulatory disturbances. The general aspects of neoplasia are discussed in full. Entirely absent is the correlation of tissue reactions to specific disease. For instance, although the development and retrogressive changes of a tubercle are described as an example of chronic inflammation, the pathological syndromes that occur in tuberculosis are omitted, as well as any discussion of other conditions that stimulate tubercle formation.

Morphological descriptions are brief, but are supplemented by excellent illustrations. There is a good bibliography for further reading in experimental pathology. Especially valuable are the discussions of the experimental aspects of controversial subjects in pathology. Thus, in spite of the fact that this volume's usefulness is limited by its omissions, medical students, research scholars, pathologists, physiologists, and clinicians will find it a valuable supplement to the usual pathology textbook.

ELLA H. OPPENHEIMER

YOU AND YOUR HEART. *A Clinic for Laymen on the Heart and Circulation.*

By H. M. Marvin, T. Duckett Jones, Irvine H. Page, Irving S. Wright, and David D. Rutstein; foreword by Paul D. White. Random House, New York. $3.00. xii + 306 pp.; ill. 1950.

You and Your Heart is a professionally competent, nonmedical presentation of heart disease by 5 outstanding physicians. The need for a popular exposition of this subject on a plane higher than *The Readers Digest* is real, for there is wide interest and much present misconception. An initial chapter of anatomy and physiology which introduces the reader to the necessary technical terminology is one of the weakest portions of the book and will distress many students of biology. Explanations in this section are in the form of broad analogies. There is too little actual information. The addition o some pictures plus a graphic description of the heart beat, heart sounds, and so forth, would perhaps elevate this chapter to the level of the remainder of the book. The chapter on the history of the subject is enjoyable and informative. The remaining sections deal in turn with congenital heart disease, coronary artery disease, psychosomatic aspects of circulatory disease, rheumatic fever, high blood pressure, arterial disease, and public health in relation to heart disease. These sections by the 5 different authors are all capably handled. It is perhaps unfortunate that the chapter on congenital heart disease, at present of such public interest, misses an important opportunity to explain the contribution of animal research and the need for it. Also unfortunate is the fact that the final chapter on misapprehensions is weak and not overly convincing. Such minor criticisms, however, are all that can be fairly leveled at this volume. *You and Your Heart* will prove absorbing reading to many with, or interested, in heart disease but without medical knowledge.

E. CONVERSE PEIRCE, 2ND

THROMBOSIS—*In Arteriosclerosis of the Lower Extremities.*

By Edward A. Edwards. Charles C Thomas, Springfield, Ill. $2.00. viii + 74 pp.; ill. 1950.

This slight volume is a brief, readable account of acute thrombosis in peripheral atherosclerosis (arteriosclerosis obliterans). According to the author it is the thrombotic occlusion, and not the underlying arterial process, which causes sudden ischemia and gangrene. The pathological findings are stressed; the clinical picture and the immediate treatment are briefly covered; and a few illustrative case reports are given.

Although generally well conceived, this volume contains no new material, and several ideas require comment. The concept of pure atherosclerosis complicated by occasional complete thrombosis appears to be incorrect. Actually both processes progress gradually together, minor non-occluding thromboses being an intimate part of the pathological sequence. The author's unreserved recommendation of lumbar sympathectomy as an emergency treatment of acute arterial occlusion is dangerous and cannot be condoned. That sympathetic denervation may shunt blood away from a diseased arterial bed initially has been repeatedly demonstrated and its use in arteriosclerosis, in the presence of actual tissue necrosis, is generally considered contraindicated.

E. CONVERSE PEIRCE, 2ND

PRACTICAL HAEMATOLOGY.

By J. V. Dacie. Chemical Publishing Co., Brooklyn. $4.50. viii + 172 pp.; ill. 1951.

This small book gives concise, specific directions for the performance of the more important laboratory procedures which are of practical value in the study of hematologic disorders. As a rule only one or at most two alternative methods are described, but these are care-

fully chosen and are obviously based on the author's extensive personal experience with them. It includes a brief consideration of disturbances of coagulation, determination of blood groups, and reactions to transfusions.

The author has indicated the clinical conditions in which the tests are useful, but only the briefest references are made to problems of differential diagnosis. A most valuable feature is a relatively detailed discussion of the errors inherent in the tests, particularly those dependent upon random distribution and sampling, which are substantially greater than is generally assumed.

The book is well written, free from padding, and should be especially useful to technicians and physicians who are actually performing or directly supervising the performance of such tests.

P. W. CLOUGH

ACUTE LARYNGOTRACHEOBRONCHITIS.

By A. Harry Neffson. Grune & Stratton, New York. $5.00. x + 197 pp.; ill. 1949.

This is a medical book devoted almost entirely to diagnosis, treatment and the like. About 20 pages are devoted in the beginning to four brief chapters on the history of "croup," its incidence, pathology, and bacteriology.

MANUAL OF TUMOR NOMENCLATURE AND CODING.

Prepared by Subcommittee of the Statistics Committee, American Cancer Society. American Cancer Society, New York. $2.50. 119 pp. 1951.

From the Preface: "The study of tumors is an exacting and complex discipline. Its pursuit is difficult enough without the handicap of barriers to communication in the form of conflicting terminologies and statistical coding systems. In preparing this manual, pathologists and statisticians have pooled their efforts to overcome these barriers, and to provide a common language for themselves and for record librarians, practitioners, students, teachers, and research workers. If the users of this booklet will approach the problem in the same spirit, the result may be real a contribution to the accurate analysis and exchange of oncological data." This is the type of publication now needed in many biological fields. The tumor workers are to be congratulated on their accomplishment.

PSYCHOLOGY AND ANIMAL BEHAVIOR

EXPERIMENTAL FOUNDATIONS OF GENERAL PSYCHOLOGY. *Third Edition.*

By Willard L. Valentine and Delos D. Wickens. Rinehart & Co., New York. $3.00. xxiv + 472 pp.; ill. 1950.

The principal goal of this revision is the same as that of two previous editions. It is designed to give the beginning student "some insight into how a psychologist goes about collecting the information he needs and what he does with it after he collects it." To this end a new first chapter, written by the late senior author, contrasts the general approaches of magic and science as they seek to account for psychological phenomena. The second and third chapters emphasize the need for controls in experimentation, particularly when the dogma of common sense or prejudice is challenged. There follow 18 chapters, expanded and revised by the junior author: Aptitudes; Inheritance; Maturation and Growth; Intelligence; The Meaning of Intelligence-Tests Scores; Physiological Conditions; Drives and Motives; Motives and Incentives; The Development of Emotional Behavior; Emotion in Adults; Suggestibility and Hypnosis; Perception (almost completely rewritten); Conditioning (reorganized); Learning (reorganized); Remembering; Reasoning; Learning, Thinking, Imagining, Dreaming; and Personality (added in this edition). In each chapter a half-dozen or so representative experiments are analyzed, illustrating the kinds of methodological problems facing the psychological investigator and the experimental procedures in current use.

The obvious function of this book is as a supplementary textbook in the elementary psychology course, where the details of experimental method must be given through reading rather than laboratory experience. But it should prove helpful as well to the general reader who desires an introduction to behavior science as it has developed during the past decade or two. The description of the 130-odd experiments brings the reader into contact with a surprising number of basic psychological principles, as well as providing numerous glimpses of newly emerging trends in research and application.

FRANK W. FINGER

PROBLEM-SOLVING PROCESSES OF COLLEGE STUDENTS. *An Exploratory Investigation.*

By Benjamin S. Bloom and Lois J. Broder. University of Chicago Press, Chicago. $2.75. 109 pp. 1950.

This monograph is a study of the mental processes used by college students in arriving at their answers to questions asked in the comprehensive examinations administered at the University of Chicago. The psychological analysis of thought processes is exceedingly difficult and elusive, and the authors are quick to point out the many limitations of their study. A striking shortcoming of the monograph arises from the way the authors have chosen to present their findings. Although the raw data of an

experiment such as this would be of great interest to scientists, few of the original protocols are given. Instead, the authors present their findings mainly as a series of conclusions. It is difficult to discover precisely how many students were studied and exactly what questions were asked of which students. As a result, the reader is likely to feel that the meat of the report has been left out.

Despite these criticisms, there is much of value here on a highly important problem. Educators will be especially interested in that part of the study which demonstrates the possibility of training students to solve problems more effectively.

A. CHAPANIS

REMEMBERING. *A Study in Experimental and Social Psychology. Reprint (First Edition 1932).*

By Frederick C. Bartlett. Cambridge University Press, New York and London. 30s. x + 317 pp. + 2 pl.; text ill. 1950.

Laboratory psychologists first studied the laws of learning and forgetting with artificial materials—nonsense syllables—in order to get at these functions in their "pure" form. Bartlett's book, published in 1932, ran counter to this kind of experimentation, because in it he dealt with experiments using meaningful forms, words and passages. An important conclusion of his work was that remembering cannot be divorced from perceiving, recognizing, and imaging, and that all of these are related to cultural factors and other aspects of social psychology. Bartlett's work is one of the classics in psychology. The present volume is a reprint, without change, of the original edition.

A. CHAPANIS

PRINCIPLES OF GENERAL PSYCHOPATHOLOGY. *An Interpretation of the Theoretical Foundations of Psychopathological Concepts.*

By Siegfried Fischer. Philosophical Library, New York. $4.75. xxiv + 327 pp.; ill. 1950.

On the first page of the preface of this book it is stated that "this book is a survey of the most important psychopathological phenomena and their theoretical bases." That it is a survey is undeniable. It is divided into four parts. Part I deals with the fundamentals of psychopathology, Part II with understandable and causal connections, Part III with syndromes or symptom-complexes of mental disturbances, and Part IV with normal, neurotic, and psychopathic personalities and the relation between personality and psychosis.

The book contains numerous definitions and classifications, the value of which is sometimes questionable. In fact, emphasis on taxonomy and its associated thought-limiting compartmentalization is strong throughout the work. Part I, entitled Fundamentals of Psychopathological Concepts, which occupies over half the volume, is entirely devoted to a systematic listing of mental factors, characteristics, processes, and disturbances. Although some may find such classification useful, one wishes that the discussion of concepts and fundamentals had been presented less as dogma and more as the consequence of a reasoned intellectual process which would stimulate the student's imagination and breadth of thought. Classification is certainly not the key to understanding.

General psychopathology is distinguished from general psychology, the latter dealing with "regularities of normal happenings," in contrast to the former, which the author states is "the science of the regularities of pathological mental happenings." Although it is perhaps not strictly relevant in a brief review, one feels that the liberal use of the term "science" in such instances as this should be of greater concern to many of us than it has been to date. The word "science" has come a long way from its original narrow and rather limited meaning, and has undergone many changes. Dynamic psychology and psychopathology may be sciences—depending upon the concepts involved, the methodological procedures used, and the interpretations made. The author draws a distinction between the natural sciences which are said to have been built on the principle of causation, and dynamic psychology which is based on "comprehensible connections." The implication is drawn that anything not based *solely* on the principle of causation cannot be a science. This is not strictly the case. However, one can find himself in agreement with the author in many cases of psychological and psychiatric discussion in which the word science is used without any excuse whatever.

Any attempt to present the concepts under discussion in a scientific way, as well as to stand them on their own "scientific feet," would have been assisted immeasurably by relating them to present-day knowledge, concepts, and theories in neurophysiology. The marked lack of such discussion in this work is a serious defect.

The sections of the book on infantile drives and the abnormal personality include some successful discussion of major problems, some of which could have been extended.

Certain changes in the exposition of the book, particularly in the directions of including related fundamental neurophysiological concepts and a more completely dynamic point of view, would seem desirable. Nonetheless, the author has succeeded in presenting a great deal of information of interest to workers in sociology, psychology, and psychiatry.

R. G. GRENELL

PRINCIPLES OF INTENSIVE PSYCHOTHERAPY.

By Frieda Fromm-Reichmann. The University of Chicago Press, Chicago. $3.75. xviii + 246 pp. 1950.

This is an amazingly helpful book, written out of the author's long years of experience in dealing with both neurotics and psychotics, and replete with practical, timely suggestions concerning the intensive treatment of both types of patients. The principles which she expounds are based on the general proposition that treatment is a collaborative effort with the physician in the position of a participant observer. She has much to say concerning the patient's needs in treatment, the physician's needs in treating, and the pitfalls encountered in the best adjustment of these two forces.

Her work carries evidences of deep inspiration from Freud and Harry Stack Sullivan particularly, but psychiatrists who bear no emotional allegiance to either one of these famous figures can agree with and learn from Frieda Fromm-Reichmann. Years ago one of America's outstanding psychoanalysts said to be casually, referring to one of American psychiatry's great figures, that he was the last of the "Menschenkenner." After reading Fromm-Reichmann, I am inclined to believe the breed is not extinct yet, and that she might very well be counted among the specimens still extant. Her genuine sympathy for sick people and her respect for them, so evident in the pages of this book, are matched only by her very real skill in bridging the gaps in rapport and understanding between herself and the patients. It would be unfortunate if this book were not to be read by every psychiatrist actively working with patients, be he a novice or an old-timer.

In elucidating her practices and theories, she comes to some drastically different conclusions about certain matters than Freud did. This will undoubtedly serve to raise controversy, but the new points of view are very welcome because they dovetail more closely into the general viewpoint of human performance and its aberrations, as expounded by Adolf Meyer in his heyday. In short, teleology is best accepted on the broadest base possible.

WENDELL MUNCIE

NEUROSIS AND HUMAN GROWTH. *The Struggle Toward Self-Realization.*

By Karen Horney. W. W. Norton & Co., New York. $3.75. 391 pp. 1950.

This restatement of Horney's views of the problems of neurosis and human growth contains chapters on the varieties of neurotic manifestations, the aims of psychoanalytic therapy, and theoretical considerations. In the last chapter, she is explicit about her deviations from the Freudian camp. The book is well written and on a level with her previous statements on the matter, and a thoughtful reader will derive considerable information concerning this important psychoanalytic deviation. Whatever one may think about the methods of treatment, there is an impressive presentation of Karen Horney's own particular view of the importance of the current problems in the patient's life. The first chapter on the morality of evolution is particularly interesting. She summarizes it as follows:

"We arrive thus at a morality of evolution, in which the criterion for what we cultivate or reject in ourselves lies in the question: is a particular attitude or drive inducive or obstructive to my human growth? As the frequency of neuroses shows, all kinds of pressure can easily divert our constructive energies into unconstructive or destructive channels. But, with such a belief in an autonomous striving toward self-realization, we do not need an inner strait jacket with which to shackle our spontaneity, nor the whip of inner dictates to drive us to perfection. There is no doubt that such disciplinary methods can succeed in suppressing undesirable factors, but there is also no doubt that they are injurious to our growth. We do not need them because we see a better possibility of dealing with destructive forces in ourselves: that of actually outgrowing them. The way toward this goal is an ever increasing awareness and understanding of ourselves. Self-knowledge, then, is not an aim in itself, but a means of liberating the forces of spontaneous growth."

WENDELL MUNCIE

ONEIROPHRENIA. *The Confusional State.*

By L. J. Meduna. The University of Illinois Press, Urbana. $2.50. xii + 100 pp. 1950.

In this monograph, Meduna describes a condition often mistaken for true schizophrenia and sometimes for manic depressive psychosis, and characterized by a disturbance in the sensorium, with faulty perceptions leading to hallucinations, delusional ideas, and thinking difficulty, and in which there is a distinct disturbance in the sugar metabolism with a resistance to insulin. These, according to the author, constitute a differentiation from true schizophrenia, in which the complete reverse of these conditions obtains. The prognosis of oneirophrenia is considered good. Meduna states that 64 per cent of full remissions were achieved with electroshock treatments within 3 to 6 months. He mentions two chronic, incurable cases which were insulin-resistant 5 to 7 years after the onset, and in another state hospital a group of 15 chronic cases in which the insulin resistance was present after 3 to 9 years. In the chronic condition, the patient's bewilderment, dread, or acute phase changes slowly to a condition of resignation and adjustment to a senseless and contradictory world. The differentiation of the disease from schizophrenia rests essentially on Bleuler's definition of primary schizophrenic characteristics, and the monograph is therefore of some importance as showing that schizoform conditions may exist which nonetheless do not correspond to Bleuler's conceptions.

It is worthwhile to point out all the subcategories possible and to bring to differential diagnosis as much diagnostic acumen as we can. The author does not state categorically whether he feels the whole condition is the consequence of the disturbed sugar metabolism, or whether sugar metabolism and the mental features are all integral elements in a syndrome with some other basic cause. What he does point out is that the fringes of the schizophrenia complex have in general a better prognosis than the hard core of schizophrenia in the classical sense as defined by Kraepelin and Bleuler. Whether this corresponds to that special group of schizophrenics with marked psychogenic etiology, reported by Bellac and others, is not clear. Suffice it to say that at least one of the cases of the author's group was psychoanalyzed for a month and thought to be neurotic and presumably there was in this case a very considerable psychogenic provocation, if that was not actually the ultimate etiology.

WENDELL MUNCIE

PERSPECTIVES IN NEUROPSYCHIATRY. *Essays Presented to Professor Frederick Lucien Golla by Past Pupils and Associates.*

Edited by Derek Richter. R. K. Lewis & Co., London. 15s. 236 pp.; ill. 1950.

This is an exceedingly interesting group of studies in honor of Professor Golla in commemoration of his seventieth birthday. The book is heavily weighted in the direction of electrophysiology and neuroanatomy and biochemistry, and very little is said regarding clinical psychiatry. There is quite a bit in the introduction to justify this, since the writers have aimed to indicate the most promising lines of advance and the goals in the fields within which they are working. The chapters dealing with the electrophysiology of mental mechanisms, electroencephalography, neural nets, the concept of the schema, perspectives in endocrinology, and so on, are extraordinarily interesting and stress an aspect of neuropsychiatric research which gets too little attention in this country. This book should be read by every psychiatrist.

WENDELL MUNCIE

TECHNIQUE OF ANALYTICAL PSYCHOTHERAPY.

By Wilhelm Stekel; translated by Eden and Cedar Paul; introduction by Samuel Lowy. Liveright Publishing Corp., New York. $4.95. xxiv + 403 pp. 1950.

This translation of Stekel's *Technik der analytischen Psychotherapie* (1938) is a very provocative book. Here we see illustrated the author's essential allegiance to the Freudian discoveries, his impatience with certain aspects of Freudian method and theory through his case histories, and the working of an intuitively gifted psychoanalyst with an urge to find shortcuts in treatment. That he found such effective shortcuts Stekel never doubted. Many others will be less sure that he did. Nevertheless, his bold, active participation in treatment left its mark, not only for practical but also for theoretical reasons, which are slowly being clarified today in the work of various schools of psychoanalytic thought.

The volume is rather polemic in phraseology at times, which is to be understood in the context of the time at which Stekel was more active than perhaps he is today. An introduction by Samuel Lowry, M.D., St. Bartholomew's Hospital, London, furnishes valuable insight into the essential importance of this volume. Stekel covers all aspects of treatment from the preliminary interview to the end of treatment, and devotes special chapters to the transference situation, treatment of the family, analysis of special neurotic states, and so on. He is perhaps more frank than many treating psychiatrists in stating that he does a job in education. This is certainly true in every treatment situation, even though some theorists would tend to deny it. The infiltration of Freudian or more general psychoanalytic thought into our current culture is clearly the result of an educative process in which individual psychoanalysts have played a part. I doubt whether one will come out of the experience of reading this book with any well-prepared system of action in any given case, but he should arrive at a better understanding of the opportunities open to a worker who chooses to participate actively in treatment, with the end in view that the central theme of the neurosis shall be discovered and the patient educated to a better performance.

WENDELL MUNCIE

THE PSYCHOANALYST AND THE ARTIST.

By Daniel E. Schneider. Farrar, Straus & Co., New York. $4.00. xiv + 306 pp. + 11 pl. 1950.

The author states that this volume is "a tentative exploration into the nature of true talent or genius and what appears . . . to be the essential attributes of genius, with some attention to those forces which inhibit, as well as encourage, its full development and to the personal dangers and advantages its possession brings." Elsewhere he refers to this as an effort "to try to forge a basic working concept valuable to an effective psychoanalytic esthetics."

The book concerns itself first with the psychoanalytic interpretation of certain artistic and literary masterpieces, starting with the plays of Sophocles, and including later analyses of *Macbeth* and Arthur Miller's two modern plays. Also included are psychoanalytic interpretations of the artistic productions of Picasso and Chagall, and references to Freud's comments on Da Vinci. With these as illustrations and drawing on his psychoanalytic experience, Schneider attempts an an-

alysis of the basic qualities in the possession of artistic talent and its use, the ends to which it is directed, the contents involved, and the forms employed. He does not go beyond Freud's comments on the artist as a person who, by constitutional disposition, possesses special talents which are directed toward putting into a compelling and universally acceptable form the contents of the unconscious self; or people with a lesser degree of talent who attempt neurotically to be artistic, having the same problems without the same skill and effective esthetic universalization. Schneider points out, for instance, that in the plays mentioned the current social implications of the plots and interplots carry added weight and provoke added tension because of their interrelations with the personal plots incident to the Oedipal development and resolution. In the artist, there is no conscious effort at psychoanalytic understanding of the problem, his conscious effort being directed toward an esthetic transformation of the unconscious material into the terms of the artistic achievement. Thus artists are portrayed as intuitive psychoanalysts, and the author believes that the Freudian discoveries have made it possible for such gifted men, acting according to Freudian postulates, to understand what artists have always been able to do intuitively through sheer genius. As for the author, undoubtedly his psychoanalytic understanding enhances the value of his esthetic appreciation. Whether this is generally true might be doubted; at least it would need further proof, I should think. Schneider draws a distinction between the real artist and the neurotic imitator of art who has a neurotic need to be an artist, and points out that the psychoanalysts cannot make an artist out of him, though they can free him of his neurotic needs; whereas for the true artist, the psychoanalyst can be of help on occasion by freeing him of certain problems so that he may use his talent to greater advantage.

The author is evidently a convinced Freudian, and not a little effort in translation into less dogmatic terms is necessary to follow the thread of his argument. Nevertheless, it is very provocative. The analyses of Sophocles' plays alone would merit the closest attention, because Schneider brings out certain aspects of the Oedipal problem not commonly stressed.

From the standpoint of one who maintains an eclectic viewpoint, and is much less qualified to talk on the subject than the author, it would seem that the masterpieces of literature portray not only universal problems, but in particular universal problems in individuals who have not made the common, puny compromises with instinct and conscience which ordinary mortals find themselves forced to make. They thus portray the strength and the weakness of us all in exaggerated degree. If the author could divest himself of his psychiatric mantle and write in non-technical terms, his ideas ought to create a real sensation in artistic circles.

WENDELL MUNCIE

SEX PROBLEMS IN SCHOOL.

By Rene Allendy and Hella Lobstein. Translated from the French by Egon Larsen. Staples Press, New York (made and printed in Great Britain). $2.00. 182 pp. 1950.

This is a small book, first published in France in 1939. It presents, essentially, the thesis that "the identification of sex and sin should cease." The normal sexual curiosity of children should be satisfied instead of repressed. If this were accomplished through the intelligent cooperation and understanding of parents and teachers who deal with the child of grammar-school age, a great deal of the intrapsychic conflict which the majority of children experience in this area could be relieved.

The authors are both psychoanalysts. They support their plea for more sound sex education on the basis of dynamic principles of the emotional development of children as described by Freud. The volume, however, is scaled to reach the lay public so that the theoretical material is used sparingly to lend weight to the author's position. The real appeal to the average reader will lie in the illustrations, chosen to show how misinformed children react to sexual knowledge with fear or distaste when it is finally forthcoming, how they are taught hypocrisy and guilt in reference to sex, and how lack of sexual information can make a child vulnerable to exploitation.

HELEN ARTHUR

EXPERIMENTS IN SOCIAL PROCESS. *A Symposium on Social Psychology. McGraw-Hill Publications in Psychology.*

Edited by James Grier Miller. McGraw-Hill Book Company, New York, Toronto, and London. $3.00. x + 205 pp. 1950.

As the title indicates, this is a collection of papers illustrative of some typical studies of social processes. The book contains 8 papers delivered at a symposium on social psychology at the University of Chicago, together with a preface by the editor and a transcript of a round table discussion on Social Psychology and the Atomic Bomb. Papers included cover the topics of Scientific Methodology in Human Relations (Donald G. Marquis), The Strategy of Sociopsychological Research (Ronald Lippitt), Laboratory Experiments: The Role of Group Belongingness (Leon Festinger), Survey Research: Psychological Economics (Dorwin Cartweight), Survey Techniques in the Evaluation of Morale (Daniel Katz), Field Experiments: Changing Group Productivity (John R. P. French, Jr.), A Comparative Study of National Characteristics (Donale V. McGranahan and Ivor Wayne), and The Implications of Learning Theory for Social Psychology (James J. Gibson).

A major concern of the authors is the methodology

by which valid investigations of complicated social phenomena can be made. Individually and together they have made an understandable presentation of the central issues of this difficult subject, emphasizing basic principles and avoiding for the most part the technical problems which arise in translating principles into detailed experimental designs. There tends to be some repetition of these points from chapter to chapter, a difficulty not easily averted in a book such as this. In most instances principles of methodology are illustrated by non-technical discussions of experiments made by the authors. While the social psychologist or social scientist in general will find little that is new in this book, the interested layman should find it a valuable introduction to the methods of social psychology, as well as a sampling of some of the important facts concerning social processes.

H. J. BOND

VOCATIONAL REHABILITATION OF PSYCHIATRIC PATIENTS.

By Thomas A. C. Rennie, Temple Burling, and Luther E. Woodward. The Commonwealth Fund, New York. 75 cents (paper). x + 133 pp. 1950.

This is a report from the Division on Rehabilitation of the National Committee for Mental Hygiene of a survey made in New York, Connecticut, and Michigan of the vocational needs and opportunities confronting the post-hospitalized psychiatric patient. The authors stress the need for vocational classes within the hospital in the framework of occupational therapy, as well as the hospital's responsibility to do everything possible to effect the social reintegration of the patient, and the function of the patient's job in the same matter. There is a list of helpful tables including rehabilitation services performed by the state and the frequency of their use, the results of rehabilitation efforts by the state, the earnings of rehabilitation patients in relation to cost, the cost of the services to the agencies involved, the work status and earnings of clients at the time of follow-up, rehabilitation in relation to diagnosis and in relation to education, and problems leading to referral.

The authors point to certain research needs arising out of this study, especially a need for a larger group of patients to be studied with complete statistical evaluation of all the items involved. They point also to the need for the rehabilitation councelor to have more adequate information about the emotional satisfactions people need to find in their jobs, and to the need for studying methods to improve the selection of clients receiving vocational training so as to discover what modifications in the training program are desirable. This is a helpful little volume.

WENDELL MUNCIE

HUMAN BIOLOGY

HAVING A BABY. *A Guide for Expectant Parents. A Signet Book.*

By Alan Frank Guttmacher; illustrated by Leon Schlossberg. The New American Library of World Literature, New York. 25 cents (paper). 191 pp.; ill. 1950.

Previously known as "The Story of Human Birth," this paper-covered edition has been considerably condensed and revised, and has been given a new introductory chapter. There is less attention to the history of childbirth and obstetrics, but nearly everything an expectant parent might want to know. Alan Guttmacher writes well, and few more entertaining and instructive books for the medical layman exist. Up-to-date topics like Rh incompatibility and its effects upon the child are accompanied by excellent advice from an authority.

CHANGE OF LIFE. *A Modern Woman's Guide.*

By F. S. Edsall. Woman's Press, New York. $2.00. 127 pp. 1949.

Mrs. Edsall has written for laywomen a simple treatment of the menopause and related topics, such as the harmony of the hormones, the detection of uterine and mammary cancer, and common psychic symptoms. Up to date in the treatment of new information, the author appears to have some difficulty in getting technical terms correct: guanozolo becomes "quanozolo," pitocin becomes "pictocin," etc. Such minor errors will not seriously impair the value of this book for its intended readers. There is an extensive and well chosen list of more advanced reading for those who are interested.

MARRIAGE AND FAMILY RELATIONSHIPS. *Revised Edition.*

By Robert Geib Foster. The Macmillan Company, New York. $2.75. xvi + 316 pp. 1950.

In the psychology of human relations those of marriage and family life are second to none. This book should aid many puzzled young people to learn better how to make the necessary adjustments. It is perhaps common sense more than science.

THE BORUCA OF COSTA RICA. *Pap. Peabody Mus. Amer. Arch. & Ethnol., Harvard Univ., Vol. XXVI, no. 2.*

By Doris Z. Stone. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, Mass. $2.50 (paper). viii + 50 pp. + 8 pl.; text ill. 1949.

The author describes this as an "introductory paper" on the Boruca Indians, who are by far the most Euro-

peanized of the Southern Costa Rican tribes. She has made an effort to record a few facts about their primitive ways of life before these disappear altogether.

BIOMETRY

STATISTICAL METHODOLOGY REVIEWS 1941–1950. *Edited by Oscar Krisen Buros. John Wiley & Sons, New York; Chapman & Hall, London.* $7.00. xii + 457 pp. 1951.

This volume is designed to assist research workers and statisticians in locating and evaluating books on statistical methodology in all fields. It lists 342 books and monographs on statistical methodology written in English during the period 1941–1950. The main part of the volume, however, consists of reviews of these books. In all, there are excerpts of 842 reviews selected from 112 journals. Although it is interesting to see how various reviewers may agree or disagree about the same book, *Statistical Methodology Reviews* is a volume with very limited usefulness. You may sometimes have occasion to consult it in a library, but unless you are a professional biometrician you will almost certainly not care to own it.

A. CHAPANIS

INTRODUCTION TO STATISTICAL ANALYSIS. *By Wilfred J. Dixon and Frank J. Massey, Jr. McGraw-Hill Book Co., New York.* $4.50. x + 370 pp. 1951.

This textbook was written for a basic statistics course to be taken by students from all fields in which statistics finds application. The only mathematical ability required of the student is a knowledge of algebraic addition, substraction, and multiplication. The illustrative samples in the text and the problems at the end of each chapter have been drawn from a variety of fields—biology, psychology, agriculture, industrial engineering, and economics.

Two features of this book distinguish it from the usual run-of-the-mill elementary textbooks. These are (a) its coverage of material, and (b) its appendix. With regard to the former, you will find here discussions of highly useful statistical techniques seldom treated in elementary books. Thus, in addition to the usual material on measures of central tendency, dispersion, correlation, the normal distribution, and statistical inference, there are chapters on the analysis of variance, analysis of covariance, non-parametric statistics (the sign test, runs, Chebyshev's inequality, and the like), sequential analysis, and sensitivity experiments. Even within the more conventional chapters there are topics which are unusual for an elementary textbook, e.g., the two types of errors involved in statistical inference (many elementary books only discuss one), normal probability paper, binomial probability paper, the efficiency of various statistics, and IBM calculating equipment. For a text which always manages to remain practical and within the grasp of the elementary student, this one has very wide coverage.

The second feature of this book which merits special attention is the appendix of 26 statistical tables, 71 pages in all. It is the best collection I have ever seen in any textbook. For example, not only is there a 5-page table of random numbers, but there are also 3 tables, 20 pages in all, of random *normal* numbers (with $M = 0$, $\sigma = 2$; $M = 0$, $\sigma = 1$; and $M = 2$, $\sigma = 1$). Such tables are hard to find anywhere. As another illustration, the F-table is given for 4 significance levels, 5%, 2.5%, 1%, and 0.5%. Most commonly this table is given for only the 5% and 1% levels.

In summary, this is an eclectic introductory textbook of unusual merit because of its wide coverage of statistical techniques. Primary emphasis throughout is on the practical use of statistics.

A. CHAPANIS

DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

LABORATORY DESIGN. *National Research Council Report on Design, Construction and Equipment of Laboratories. Edited by H. S. Coleman; introduction by Roland Wank. Reinhold Publishing Corp., New York.* $12.00. x + 393 pp.; ill. 1951.

This book is meant to serve as a "source of constructional information on laboratories." Its aim is to present "authoritative up-to-date advice and essential data on the design, location, construction and equipment of laboratories for research and educational institutions and for the industries." It has been produced under the auspices of the National Research Council.

Part I discusses materials, facilities, services, and equipment; Part II deals with teaching laboratories; Part III with industrial laboratories; and Part IV presents concise descriptions of some modern laboratories—in both university and industry. Anyone planning new laboratories will certainly find help in this series of discussions. For the most part the plans and drawings shown are quite good, but many of the photographs are very cluttered and of little value.

R. G. GRENELL

APPROVED LABORATORY TECHNIQUE. *Fifth Edition. By John A. Kolmer, Earle H. Spaulding, and Howard W. Robinson. Appleton-Century-Crofts. New York.* $12.00. xii + 1130 pp. + 28 pl.; text ill. 1951.

Any book on laboratory technics is in constant need of

revision, as new and better methods are always being developed. This revision of a universally accepted standard medico-public health laboratory text is very well done. Particularly gratifying is the stress given in the Preface to the importance of accurate laboratory results and the value of inter- and intra-state surveys on improving the performance of tests done in various laboratories.

Among some of the new topics included in this edition are phase microscopy, the nomenclature of cells and diseases of the blood and blood-forming organs proposed by the Committee for the Clarification of Nomenclature, the Papanicolaou cytodiagnosis of cancer, the VDRL method of quantitative estimation of spinal fluid protein, the *Rana pipiens* urine hormone test for pregnancy, many new and improved culture media, methods for testing the susceptibility of bacteria to various antibiotic compounds, newer methods in the rapidly developing field of virology, laboratory diagnosis of toxoplasmosis, tests for Rh agglutinins, blocking antibody and types of the Rh factor, skin tests for histoplasmosis and drug allergies, etc. There are more and better illustrations and color plates.

It is rather disappointing to note that while many of the newer bacteriological media, using the known peptones, are given, the poorer old-type media, using beef extracts and infusions, are still included. A choice of methods or media is given in many instances. The charts and tables of normal values are most valuable. In fact, no laboratory should be without this book, as it contains a wealth of material in a very accessible form.

E. PETRAN

THE OVERTHROW OF THE PHLOGISTON THEORY. *The Chemical Revolution of 1775–1789. Harvard Case Histories in Experimental Science—Case 2.*

Edited by James Bryant Conant. Harvard University Press, Cambridge, Mass. 90 cents (paper). 59 pp. 1950.

The purpose of these case studies in the history of experimental science is given in the Foreword. The appreciation of the methods of the experimental sciences by any non-scientist is nowadays fraught with great difficulty. Conant and the Harvard group feel that in the science of an earlier day, not so impossibly complex, it is easier to appreciate the concepts and conceptual schemes of science, to see how speculative ideas become broad working hypotheses, and how the latter lead to the testing of deductions by experimentation. The case studies also reveal the relation of the advance of science to progress in the practical arts and to the social and philosophical atmosphere of the time. Certainly no case study is better suited to do these things than that of the overthrow of the phlogiston theory. Biologists as well as chemists should find the treatment of this case history both absorbing and stimulating.

BENTLEY GLASS

REPORT OF THE EXECUTIVE COMMITTEE 1950. *International Council of Scientific Unions.*

Edited by F. J. M. Stratton. Cambridge University Press, London and New York. 5s. (paper). viii + 78 pp. 1951.

THE QUARTERLY REVIEW OF BIOLOGY publishes critical reviews of recent researches in all of the special fields of biological science. The contribution should present a synthesis or digest of the researches and a critical evaluation of them. A mere synopsis of the literature without evaluation or synthesis is not desirable.

Theoretical papers are published occasionally, especially when such papers (1) include a critical synthesis of the literature bearing on the theory and (2) are likely to promote further research in a given field.

The article should be written in concise language, yet in sufficiently non-technical form as to be intelligible not only to specialists in other fields but to the general biologist as well. To this end the article should have a general introduction and a summary which enumerates one by one all of the principal facts and conclusions given in the paper. Interpretative diagrams and schemes are very desirable.

Material ordinarily taking the form of footnotes is set in small print and placed in the text and consequently should be written in a style so as to fit readily into the text. Acknowledgments are printed in the text in small type at the end of the article just preceding the List of Literature. Recent issues of the Quarterly should be examined for style as regards (1) section or subsection headings in the text, (2) literature citations in the text, and (3) List of Literature.

The subjects and authors of articles are selected by the Editors and members of the Advisory Board. Unsolicited articles which conform with the objectives of the Quarterly will be considered for publication.

A feature of the REVIEW is the section dealing with *New Biological Books*. In this department the book literature of different countries in the field of Biology is given prompt notice.

The QUARTERLY REVIEW OF BIOLOGY is issued in March, June, September and December.

Twenty-five reprints, with covers, of articles will be furnished to contributors free of cost. The reprint order blank accompanying galley proofs gives the cost of additional reprints.

Manuscripts **may be sent to** Dr. B. H. Willier, Department of Biology, The **Johns Hopkins University, Baltimore 18, Maryland.**

Books for Review may be sent to Dr. H. B. Glass, Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland.

New subscriptions and renewals **are entered to begin with the first issue of the current volume. Should any issue of the current volume be out of print at the time the subscription order is received, the pro-rata value of such numbers will be refunded to the subscriber.**

Subscriptions should be renewed promptly—To avoid a break in your **series, subscriptions should be renewed promptly. The publishers cannot guarantee to supply back issues on belated renewals.**

Subscription price: $6.00 United **States and countries within the Postal Union; $6.50 countries outside the Postal Union.** Single copies **will be supplied, when available, at the rate of $1.75 a copy.**

Claims for copies lost **in the mails must** be received within **30 days (domestic).**

Changes of address must be received at least two **weeks** prior to **the date of issue.**

THE WILLIAMS & WILKINS COMPANY

Publishers of Scientific Books and Periodicals

BALTIMORE, U. S. A.

CONTENTS

The Environmental
—*By W. D. Billings* (251–265)

Recent Advances (*to be continued*)
—*By P. Korringa* (266–308)

New Biological Books
Reviews and Brief Notices (309–337)